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The Elisha Mitchell Scientific Society

Founded in 1883 through the efforts of Francis Preston Venable

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JOURNAL
OF THE
Elisha Mitchell Scientific Society

Volume 72 November 1956 No. 2

PROCEEDINGS OF THE FIFTY-THIRD ANNUAL MEETING OF THE NORTH CAROLINA ACADEMY OF SCIENCE

The fifty-third annual meeting of the North Carolina Academy of Science was held at the University of North Carolina, Chapel Hill, on March 23 and 24, 1956.

The Academy met in its first session at 10:30 a.m. on March 23 with President E. C. Cocke presiding. A general session of three invited papers was held on this occasion.

The business meeting of the Academy was held at 4:30 p.m. at which the following business was transacted:

The minutes of the 1955 meeting were approved as published in the Journal of the Elisha Mitchell Scientific Society **71:** 157–179.

Report of the Executive Committee

The Executive Committee met at the Pines Restaurant, Chapel Hill, on March 22 at 7:30 p.m. At this meeting the following matters were considered:

1. The Committee recommended the amendment of the constitution so that contributions of sustaining members and patrons may be used at the discretion of the Executive Committee rather than for research grants only.
2. The committee also recommended that an attempt be made to coordinate the annual meeting date of the Academy with a meeting of the N. C. Section, A.C.S. when the Academy meets at Chapel Hill, Durham, or Raleigh and that, when meetings are held elsewhere, the other sections of the A.C.S. in the state be invited to plan meetings which will be coordinated with the Academy meeting.
3. Support for the Collegiate Academy should be continued to the extent of $50 for next year's program if needed.
4. Dr. H. W. Jensen was appointed to develop plans for a suitable seal or insignia for the Academy to be used on its stationery and certain publications.
5. The incoming Executive Committee was asked to study the possibilities of setting up a travel expense budget for the Secretary-Treasurer.
6. The Secretary-Treasurer was asked to approach Mrs. J. B. Derieux with the suggestion that the Derieux Memorial Award be used in the Collegiate Academy activities rather than for the physics essay.
7. The Academy should recommend to the North Carolina State Board of Education that at least one natural scientist be included on the certification board for teachers of science in the public schools of the state.

8. The Committee recommended that the Academy accept the invitation of Wake Forest College to meet on its new campus in Winston-Salem next year at a date to be determined by the new Executive Committee. This date has since been set as May 3 and 4, 1957.
9. The following were elected to membership in the Academy or reinstated to active membership:

Ahles, Harry E., University of N. C., Chapel Hill
Ashworth, Ralph P., Mars Hill College, Mars Hill
Baldwin, William P., Jr., Summerville, South Carolina
Banister, Arthur W., N. C. State College, Raleigh
Banks, William M., A. & T. College, Greensboro
Baraff, Gene A., N. C. State College, Raleigh
Beal, Ernest O., N. C. State College, Raleigh
Bernard, Dr. Richard R., Davidson College, Davidson
Bowman, James T., Jr., Duke University, Durham
Brask, Miss Sannah Ardith, Duke University, Durham
Brown, Edmond Joseph, N. C. State College, Raleigh
Burgess, Mrs. Mary Elmore, Waynesville
Burgess, Yates, Waynesville
Chen, Dr. Tze Tuan, Duke University, Durham
Daniel, Charles P., High Point College, High Point
DeLoach, Dr. Will Scott, Catawba College, Salisbury
Duke, James A., Raleigh
Edwards, Dr. Donald Anderson, A. & T. College, Greensboro
Emory, Dr. Samuel T., University of N. C., Chapel Hill
Ferenczi, Dr. Istvan, N. C. State College, Raleigh
Funderburg, John B., N. C. State College, Raleigh
Galloway, Carl W., Snow Hill
Gentry, Dr. Ivey C., Wake Forest College, Wake Forest
Greene, Miss Janice L., Woman's College of U. N. C., Greensboro
Harton, Frank N., Charlotte
Hindes, Mrs. A. L., Cameron
Hirschmann, Dr. Hedwig, N. C. State College, Raleigh
Hollar, Robert Paul, Atlantic Christian College, Wilson
Holloman, Roger E., Rich Square
Holt, Miss Jane P., Peace College, Raleigh
Horton, James H., University of N. C., Chapel Hill
Hull, Dr. Wayland E., Duke Univ. School of Medicine, Durham
Johnson, Ralph Bernard, Catawba College, Salisbury
Knisely, Dr. William H., Duke Hospital, Durham
Lackey, Mrs. Kathryn P., Hickory
Lehman, Dr. H. E., University of N. C., Chapel Hill
Lineberry, Dr. R. A., High Point College, High Point
Llewellyn, Clement Manly, Jr., Atlantic Coast Line Railroad, Wilmington
Manly, J. O., Pfeiffer College, Misenheimer
Martin, Mrs. Robert R., Calypso
McCollum, Mrs. Doris W., Madison
Morgan, Miss Bonny Lynn, University of N. C., Chapel Hill
Naylor, Aubrey W., Duke University, Durham
Neff, Miss Dorothy G., Stanfield
Nielsen, Walter M., Duke University, Durham
Nolstad, Dr. Arnold R., N. C. State College, Raleigh

Olewine, Donald Austin, School of Medicine, U. N. C., Chapel Hill
Osaki, Dr. Humio, Duke University, Durham
Palmatier, Dr. E. D., University of N. C., Chapel Hill
Ridenhour, Miss Margaret, Lenoir Rhyne College, Hickory
Robinson, Kent, Boone
Runnion, Mrs. Hannie G., Charlotte
Saunders, Mrs. Louis A., Albemarle
Schacht, Lee Eastman, University of N. C., Chapel Hill
Sharp, Christopher S., Charlotte
Silliman, Miss Frances E., University of N. C., Chapel Hill
Slifkin, Lawrence M., University of N. C., Chapel Hill
Spivey, Mrs. Doris Clemmer, N. C. Orthopedic Hospital, Gastonia
Strong, Dr. Paschal N., Jr., V. A. Hospital, Durham
Thompson, Miss Eunice A., Duke University, Durham
Tyndall, Dr. Jesse P., Atlantic Christian College, Wilson
Upstill, David A., Greensboro
Vause, Dr. Robert Z., Vanderbilt University, Nashville, Tenn.
Wall, Mrs. Margaret Y., Greensboro
Wallace, Arch Nicholson, Warren Wilson College, Swannanoa
Wells, Harry W., Duke University, Durham
Withers, John Dudley, Barber-Scotia College, Concord
Wood, Charles D., School of Medicine, U. N. C., Chapel Hill
Yarbro, Dr. Claude L., University of N. C., Chapel Hill
Youngs, Dr. Lillian Margot, University of N. C., Chapel Hill

The above reports and actions of the Committee were approved by the Academy in its business session on March 23, 1956.

TREASURER'S REPORT

Financial Statement as of July 1, 1956

Receipts

Checking account balance, adjusted, from July 1, 1955 (Security National Bank, Raleigh)	$311.04
Special income	
Ornithology Essay Awards (District and State)	160.00
Wildlife Essay Awards (District)	70.00
Physical Science State Fair Awards (Cardinal Products, Inc.)	100.00
Biological Science State Fair Awards (Carolina Biological Supply Co. and J. D. Taylor)	100.00
District Fair Awards (Southern School Supply Co.)	40.00
Printing of Brochures, State Fairs (Southern School Supply Co.)	103.31
Research Fund from A.A.A.S.	79.50
Entry Fee, National Fair (Carolina Power and Light Co.)	175.00
Collegiate Academy gifts for CANCAS (Sigma Xi chapters at Duke University, N. C. State College and University of North Carolina, $50 each)	150.00
Collegiate Academy Fund Deposit	36.18
Return on one meal, High School Science Committee	1.75
Cashier's error—Annual Meeting	.50
N. C. Psychological Association (copies of annual program)	6.00
N. C. Section, American Chemical Society	75.00
Central Section, American Chemical Society	30.00
Carolina Geological Society	25.00
Gifts from members	5.40

Dues from membership, 1956 (1955 and 1957)	1422.60
Total	2891.28
Expenditures	
Ornithology Essay Awards (District and State)	160.00
Wildlife Essay Awards (District)	70.00
Science Fair Awards (District and State)	240.00
Collegiate Academy, second place Award	15.00
Derieux Memorial Award	50.00
Entry Fee, National Science Fair	175.00
Research Grant (A.A.A.S.)	79.50
CANCAS (Collegiate Journal, two issues)	140.00
Postage, Stationery, Office Supplies	296.08
Expenses annual meeting, 1956	18.07
Expenses of High School Fair Committee	184.06
Printing of brochure for High School Science Fairs	103.31
Printing, all other	180.44
Bank charges	none
Secretarial Aid	75.83
Secretary's Commission (balance on 1954–55)	1.95
Secretary's Commission, 1955–56	142.00
Telephone (long distance calls)	37.79
Reprints of 1955 Proceedings of Academy	7.35
Bad check	2.50
Academy Conference dues, 1954, 1955 and 1956	15.00
Expenses for representation at AAAS	25.00
Elisha Mitchell Scientific Society	562.50
Total	2581.38
Bank Balance, July 1, 1956	309.90
	2891.28

Savings Account (Security National Bank, Raleigh)

Balance, July 1, 1955	$8.78
No interest to July 1, 1956	none
Present Balance	8.78

Total Assets

Checking Account	$309.90
Savings Account	8.78
Raleigh Building and Loan Account	317.62
Total	636.30

On the 10th of July, 1956, we, the undersigned, examined this account and found it to be correct.

(Signed) ARTHUR KELMAN, *Chairman*
GENNARD MATRONE
J. LEWIS ALLISON

THE POTEAT AWARD

The award for this year was given to the best paper presented before the Zoology Section. Because there were two sessions of the Zoology Section this year, a committee was asked to select the winning paper. That paper was "An electron microscope study of the growing surface of mollusc shell" by Tadashi Tsujii, D. Gordon Sharp, and Karl M. Wilbur, of Duke University.

REPORT OF THE CONSERVATION AND LEGISLATIVE COMMITTEE

The past several months have been marked by a considerable increase in activity on the part of numerous individuals and groups who wish to exploit or to develop our natural resources. In the opinion of your committee, some of these activities have not been in the public interest.

On November 29, Secretary of the Interior Douglas McKay announced that the department was abandoning plans for the controversial Echo Park Dam in the Dinosaur National Monument. This withdrawal by the Secretary represents a major victory by the Conservationists in their fight to protect the integrity of the National Park System.

The almost successful raid on the public lands by certain grazing interests were finally defeated in conference where North Carolina's representative, Harold D. Cooley, supported by other conservation-minded congressmen and senators struck out the amendment which had been tied to the totally unrelated Farm Subsidy Bill in the Senate. The amendment was vigorously opposed in the Senate by Senator Samuel J. Ervin and several other senators.

The Al Sarena case, in which Al Sarena Mines, Inc., of Trails, Oregon, became owner of 300 acres of fine Oregon timber worth more than $600,000.00 by getting the Department of the Interior to approve some questionable mining claims, is being investigated by North Carolina's Senator Kerr Scott.

What amounts to a lifting of restrictions on the exploration for oil on wildlife refuges by the Secretary of the Interior has created considerable apprehension among wildlife biologists throughout the nation. It is felt that the manner in which the Lacassine Waterfowl Refuge was opened to Frankfort Oil Company, a subsidiary of Seagrams' Distillers, should be the subject of a thorough congressional investigation.

The attempt by the Army to appropriate a portion of the Wichita Mountains Wildlife Refuge as a target area for atomic cannon is of grave concern to conservationists, particularly in view of the fact that public testimony shows that the area is not essential for national defense. If this tract of 10,700 acres is turned over to the Army, it would be possible under current law and practice for it to become a hunting preserve for a select group of Fort Sill and other army personnel and their guests in addition to its use as an impact area for artillery practice. Fire resulting from shell bursts would be almost impossible to control during certain seasons and would spread to the remainder of the Wichita refuge. The efforts by Senator Hubert H. Humphrey of Minnesota in opposing this transfer are most gratifying to conservationists.

Another resolution for the Academy's action deals with the danger to the National Wildlife Refuge System in the power now vested in the Secretary of the Interior to dispose of any or all of these refuges by signing an "administrative order" without reference to the Congress or to the public.

The continuation and strengthening of the Water Pollution Control Act (Public Law 845, 80th Congress), which expires on June 30, 1956, is recommended by your committee. A resolution is submitted for your consideration.

HARRY LEGRAND
WANDA S. HUNTER
T. E. MAKI
F. S. BARKALOW, JR., *Chairman*

A Resolution on the Wichita Mountains Wildlife Refuge

WHEREAS, the land now constituting the Wichita Mountains Wildlife Refuge was set aside in 1905 by President Theodore Roosevelt to preserve for future generations this tract as a National Forest, and because of the importance of this tract as a wildlife refuge and recreational area it was transferred to the Fish and Wildlife Service in 1935; the reduction in the size of the refuge as requested by the Army and proposed by legislation now in Congress will seriously impair, if not destroy, the value of this wildlife refuge which protects one of the largest herds of bison and Texas longhorns on the North American continent; the Secretary of the Interior has firmly opposed suggestions that a portion of the Wichita Refuge be transferred to the Army, and testimony before the Congress by the Hon. Hubert H. Humphrey calls attention to the fact that all prominent conservation groups of the State of Oklahoma and every major national conservation group are on record as opposing this transfer which is not essential to the national defense;

NOW, THEREFORE, BE IT RESOLVED, that the North Carolina Academy of Science, meeting in Chapel Hill on March 23, 1956, vigorously opposes H.R. 9665 by Congressman Victor Wickersham, and S. 3360 by Senators A. S. Mike Monroney and Robert S. Kerr, which would transfer to the Army certain lands from the Wichita Mountains National Wildlife Refuge; and that copies of the Academy's views be sent to the House Committee on Merchant Marine and Fisheries and the Senate Committee on Armed Services and that a copy of this resolution be transmitted to all members of Congress from North Carolina.

A Resolution on Water Pollution Control

WHEREAS, Public Law 845 (80th Congress) provided for a Federal water pollution control program which has been of considerable benefit to the states in their efforts to establish and carry out pollution control programs by making available technical assistance, research and grants-in-aid; the provisions of Public Law 845 expire on June 30, 1956, which will terminate Federal activity in this important work unless the present Congress enacts legislation as proposed in H.R. 9540, 84th Congress, 2nd Session, extending the Federal water pollution control program; and experience has demonstrated that there is a critical need for extending

and strengthening the Federal program, particularly with respect to the support of State water pollution control programs;

NOW, THEREFORE, BE IT RESOLVED, that the North Carolina Academy of Science, meeting in Chapel Hill on March 23, 1956, supports in principle the water pollution control program developed by the Public Health Service under P. L. 845, and urges Congress to enact necessary legislation to extend and strengthen the Federal stream pollution control program; and that copies of the Academy's views be sent to the committee on Public Works and that a copy of this resolution be transmitted to all members of Congress from North Carolina.

A Resolution on Disposition of Wildlife Refuges

WHEREAS, the National Wildlife Refuge System is essential to the protection of many endangered species of native birds and mammals and also serves to insure protection for migratory species in critical parts of their range; these refuges were established for the purpose of protecting the remnants of this nation's once vast wildlife heritage which belongs to all the people; the Secretary of the Interior has the authority to dispose of this nation's wildlife refuges by signing an administrative order without public hearings, without advance notice, or without discussion with the sportsmen and other conservationists whose funds and support were responsible for the establishment of the refuge system for the benefit of the present and future generations; and legislation (S. 2101, H.R. 5306, and H.R. 6723) is now being considered which, if passed, will require the Secretary of the Interior to obtain prior approval of the Congress before the Secretary can dispose of or relinquish any of the national wildlife refuges, or parts thereof;

NOW, THEREFORE, BE IT RESOLVED, that the North Carolina Academy of Science, meeting in Chapel Hill on March 23, 1956, supports in principle S. 2101 introduced by Senator Hubert H. Humphrey, H.R. 5306 introduced by Congressman Lee Metcalf, and H.R. 6723 introduced by Congressman Henry S. Reuss, and urges the immediate passage of legislation to require the Secretary of the Interior to obtain approval of the Congress before he can dispose of, relinquish, or permit incompatible uses of a national wildlife refuge or parts thereof; and that copies of the Academy's views be sent to the House Committee on Merchant Marine and Fisheries and the Senate Committee on Interstate and Foreign Commerce and a copy of this resolution be transmitted to all members of Congress from North Carolina.

The North Carolina Academy of Science unanimously approved these three resolutions at its annual business session on March 23, 1956.

REPORT ON THE ACADEMY CONFERENCE

The Academy Conference held its 1955 meeting on Dec. 28 in Atlanta along with the annual A.A.A.S. meetings in that city. The morning session was devoted to routine business and the reports of activities of the co-operating academies. Thirty-one delegates representing twenty-six academies were in attendance. One important item of discussion concerned the use of research funds handed to

academies by the A.A.A.S. This organization originally had stated that such funds must in 1957 and thereafter be used for high school students only. After the morning's discussion, however, the A.A.A.S. committee in charge amended its requirement so that participating Academies may use research money for either high school students or college students, preferably the former.

The afternoon session dealt with the activities of academies in the new Science Teaching Improvement Program being conducted by A.A.A.S. with Dr. John R. Mayor as director. Dr. Mayor, Mr. Wayne Taylor of Texas, former Academy Conference President, and Dr. R. W. Lefler of Indiana, constituted the panel on this program. The traditional banquet for Academy Conference representatives was given in the evening by the A.A.A.S. Our president, Dr. E. C. Cocke, and Secretary-Treasurer, Dr. John A. Yarbrough, represented the N. C. Academy.

REPORT ON THE COUNCIL OF THE A.A.A.S.

Two meetings of the Council of the A.A.A.S. were held in Atlanta on Dec. 27 and 30, 1955. At the first meeting, new officers were elected as follows: President-elect, Dr. L. H. Snyder of the University of Oklahoma; members of the Board of Directors, Dr. Paul M. Gross of Duke University and Dr. George R. Harrison, M.I.T. Dr. Paul J. Kramer, Duke University, was elected Vice-President for Section G—Botanical Sciences. Of much interest is the fact that a new headquarters building for the A.A.A.S. is nearing completion in Washington. The building is to cost about $800,000, most of which is already available.

Much interest was manifested at the second session in a report of the Resolutions Committee, headed by Dr. Harold H. Plough, relative to places of meeting in the future. Many were not willing for A.A.A.S. to meet in cities where racial segregation is observed. Finally the delegates delayed their vote but later, voting by mail, adopted the resolution of the Committee which reads as follows:

> The American Association for the Advancement of Science is a democratic association of all its members; no one is barred from election because of race or creed. All members are privileged to co-operate freely in the fulfillment of the Association's high objectives which are the furtherance of science and human welfare. No member is limited in his service because of race or creed.
>
> In order that the Association may attain its objectives, it is necessary and desirable that all members may freely meet for scientific discussions, the exchange of ideas, and the diffusion of established knowledge. This they must be able to do in formal meetings and in informal social gatherings. These objectives cannot be fulfilled if free association of the members is hindered by unnatural barriers.
>
> Therefore be it resolved that the annual meeting of the American Association for the Advancement of Science be held under conditions which make possible the satisfaction of those ideals and requirements.

Dr. John A. Yarbrough represented the N. C. Academy at these sessions.

REPORT ON THE COLLEGIATE ACADEMY

The important events of the Collegiate Academy year 1955–56 are:

1. Appointment of Dr. F. John Vernberg, Duke University, as co-sponsor in charge of the spring meeting.

2. Meeting of the Executive Committee at the Woman's College in Greensboro on October 22, 1955. Representatives, either student or faculty, from the following colleges, attended: Atlantic Christian, Catawba, Duke, Flora Macdonald, Greensboro, Guilford, Meredith, University of North Carolina, and Woman's College.

3. Publication of the first printed issue of *Cancas*—8 pages, in December, 1955.

4. Field trip to the Nuclear Reactor, Raleigh, Feb. 11, 1956, planned and executed by Dr. Amy LeVesconte, Flora Macdonald. About 80 students were present.

5. Publication of the second printed issue of *Cancas*, March, 1956, 12 pages, made possible by contributions from Sigma Xi Chapters.

6. Meeting of the Collegiate Academy, March 23, 1956, as a part of the North Carolina Academy of Science meetings. A luncheon in Lenoir Hall, attended by about 40 students, was followed by a short talk by Dr. H. S. Roberts of Duke University on "The Increasing Shortage of Scientific Personnel." At the afternoon meeting, five papers were presented, and new officers were elected: President, William Owens, Atlantic Christian College; Vice-President, Charles Dickens, Duke University; Secretary-Editor, Rachel Haralson, Woman's College U.N.C.

The paid-up members for the year were 35 individuals and 5 clubs. The colleges represented this year are: Atlantic Christian, Catawba, Davidson, Duke, East Carolina, Flora Macdonald, Guilford, Meredith, North Carolina State, Pfeiffer, University at Chapel Hill, Wake Forest, Woman's College, U.N.C., West Carolina.

CHARLOTTE DAWLEY

At the session of the Collegiate Academy on March 23 first place award for the best paper went to William G. Dotson of Wake Forest College and second place to David K. Meriney of the Department of Zoology, Duke University. The Carolina Biological Supply Company provided a $25 prize for the first place winner and the Academy a $15 prize for the second place winner.

REPORT OF THE RESOLUTIONS COMMITTEE

Be it resolved that the North Carolina Academy of Science express to Chancellor R. B. House, the other members of the administrative staff, the faculty, and students of the University of North Carolina its thanks and appreciation for their hospitality; and to them and especially to the local committee, thanks for the many services and excellent arrangements that have helped so much to make this a pleasant and well organized meeting. Be it further resolved that a copy of this resolution be incorporated into the minutes of the Academy and that copies be sent to Chancellor House and to the Chairman of the Committee on Arrangements.

L. A. WHITFORD

The above resolution was unanimously approved by the Academy.

Memorials to the following members were read before the Academy: Charles William Edwards, Zeno P. Metcalf, Milton L. Braun, Coy T. Phillips, Miss

Cornelia Strong, and Helge Lundholm. The memorials were approved by a rising vote of the members.

CHARLES WILLIAM EDWARDS

In the passing of Professor Charles William Edwards, the North Carolina Academy of Science has lost one of its oldest and most valuable members. As a charter member of the Academy, he served as chairman of the local arrangements committee when the organization held its first session at Trinity College on November 28–29, 1902. In 1903, Professor Edwards was elected the second president of the Academy.

A gifted teacher of physics, he served Trinity College and Duke University for 46 years, joining the faculty in 1898 as the first and only professor of physics at that time. He retired in 1944 as professor emeritus of physics.

Professor Edwards devoted the major portion of his life to the causes of education, particularly the advancement of physics. He early recognized the importance of science instruction in our secondary schools. Members of the Academy will recall his tireless efforts in bringing physics to the high schools of the state through demonstration lectures. For many years he responded to that call. There are many who are grateful to him for doing what he could in exciting their interest in science. As members of the Academy, which is, in this day, currently very much interested in this recurring problem, we here record this example and contribution with deep appreciation.

Throughout his active years up until a few years before his retirement, Professor Edwards was Chairman of the Physics Department of Trinity College and Duke University. He there laid the foundation on which that department has grown.

Professor Edwards' contribution to science extended beyond the boundaries of North Carolina. He was one of the important members of a small group which organized the Southeastern Section of the American Physical Society, serving as its Chairman in 1943. The physicists of the Southeast, as well as members of this Academy, are grateful for the role he played in this organization, destined to serve and to foster effectively this basic science as it has grown in importance in these more recent years.

I. E. GRAY

ZENO PAYNE METCALF

Zeno Payne Metcalf died at his home at Raleigh, N. C., January 5, 1956. Even though he had suffered poor health for many months, he died quite suddenly and unexpectedly while talking to his wife and daughter.

Dr. Metcalf was a tireless worker and continued pushing himself to the utmost to the very last, as he was in his office working on the catalog of the Homoptera of the world until noon of the day he passed away. He devoted his whole professional life to State College and brought international repute to the institution.

On March 11, 1955, Dr. Metcalf was presented the Oliver Max Gardner Award as, "That member of the faculty of the Consolidated University of North Caro-

DR. Z. P. METCALF

lina who during the current scholastic year has made the greatest contribution to the human race."

Dr. Metcalf was the author of nine books and an active member of 36 learned and professional societies. He was a key speaker at the International Congress of Zoology which convened in Paris in July, 1948, and at the International Congress of Entomologists which met in Stockholm in August, 1948. In addition he was president of three major national scientific organizations, the Entomological Society of America, the Ecological Society of America and the American Microscopical Society—a distinction accorded few scientists in the United States.

Dr. Metcalf also served on the editorial boards of four of the large national professional journals and was the author of 96 professional publications. At the time of his death he was engaged in preparing a 42-volume catalog of the Homoptera of the world. Fifteen volumes had been or were in press at the time of his death, and several more volumes are nearly ready to go to press. An attempt is being made to provide means of completing the entire set of 42 volumes. Dr. Metcalf has spent much of the past 40 years in collecting notes for the series. In an effort to obtain material, he read and checked over 20,000 books and papers dealing with insects and visited all the principal libraries in the United States and England. The order Homoptera comprises about 4,000 described genera and 30,000 described species. The catalog now contains 512,000 references, and is probably the greatest catalog of any order of insects to be found anywhere in the world.

A native of Lakeville, Ohio, Dr. Metcalf was educated at Ohio State University, where he received his A.B. degree in 1908, and at Harvard University, where he earned his D.Sc. degree in 1924.

Prior to joining the State College Faculty in 1912 he was an Instructor in Entomology at Michigan State, 1907–1908, and was on the staff of the N. C. State Department of Agriculture from 1908 to 1912. He joined the N. C. State College Faculty as Entomologist with the Experiment Station and as Professor of Zoology and Entomology. He was Visiting Professor in the summer session of Ohio State in 1916 and 1918 and in the summer session of the University of Michigan in 1926. During the school year of 1935–36 he served as Visiting Professor of Zoology at Duke University. Dr. Metcalf was Head of the Department of Zoology and Entomology, N. C. State College, from 1912–1950. He was Director of Instruction in the School of Agriculture at N. C. State College during the years 1923–1944; Director of Graduate Studies at the College, 1940–1943, and Associate Dean of the Graduate School of the Consolidated University, 1943–1950. He retired from administrative duties in 1950 and later devoted his full time to teaching, research and writing. In his latter years of teaching he was the William Neal Reynolds Professor of Zoology and Entomology.

He was active in both civic and professional affairs and was a former president of the N. C. Academy of Science and a past-president of the Raleigh Kiwanis Club. He was also a Fellow of the American Association for the Advancement of Science and the Entomological Society of America.

Dr. Metcalf was married to Miss Mary Luella Correll of Wooster, Ohio, on October 20, 1909. He is survived by his wife and by his daughter, Mrs. Katherine Brown.

CLYDE F. SMITH

MILTON LAU BRAUN

Milton Lau Braun, Professor of Physics at Catawba College from 1930 to 1955, was a graduate of Wake Forest College and the University of North Carolina, receiving the Doctor of Philosophy degree from the latter university in 1930. He taught in the high schools of North Carolina, and a mission school in China, prior to his membership on the Catawba College faculty.

Dr. Braun was a member of the American Physical Society, the American Institute of Physics, the American Meteor Society, the North Carolina Academy of Science, the Society of the Sigma Xi, and a Fellow of the American Association for the Advancement of Science. He served as president of the North Carolina Academy in 1944–46 and as chairman of the Southeastern Section of the American Physical Society in 1947–48. He was the author of numerous papers, especially on the rheological properties of rubber.

Professor Braun had many fine qualities as a teacher and scientist, among them being three particularly outstanding ones: first, his utter honesty and integrity; second, his conviction, clear to everyone who worked with him, that the discoveries of science were a revelation of God, the creator and controller of the

universe; and third, his ability to stimulate interest and hard work in his students, many of whom have completed advanced degrees in the field of physics.

His students, his colleagues, and his friends have suffered a great loss in his untimely death.

HANSEL L. HUGHES

COY TATUM PHILLIPS

Coy Tatum Phillips, Associate Professor of Geography at the Woman's College of the University of North Carolina, died from accidental drowning on August 24, 1955, at Isle of Palms, South Carolina, where he was vacationing with his family.

Dr. Phillips was born in Forsyth County, North Carolina, on October 26, 1904. He received his early education in the schools of his community and received his A.B. degree at the University of North Carolina in 1930. He married Fay Hine in 1931. They had three sons, Harry, Grady, and Coy, Jr., and one daughter, Sylvia, who with their mother survive him.

For several years he was Science Instructor at South Junior High School and at James A. Gray High School, in Winston-Salem, and from 1937 to 1942 he was Principal of the Waughtown School near Winston-Salem. In 1938 he received his M.A. degree from the University of Colorado, and received the Ph.D. degree in geography from the University of North Carolina in 1945. In 1944 he came to the Geography Department of the Woman's College of the University of North Carolina, at Greensboro, where he taught for eleven years, until his death. During the summers of 1946, 1947, and 1948 he was Visiting Professor of Geography at Miami (Ohio) University.

A well trained and enthusiastic teacher, with a strong feeling concerning man's devastation of our natural resources, he imparted to his students sincere scholarship and a deeply sympathetic and spiritual understanding of our physical universe. Dr. Phillips was always known as a Christian gentleman, as well as a scholar.

Besides his teaching and his work on numerous important faculty committees, Dr. Phillips found time for devoted work with civic and church groups in the community. He was an active member of the Association of American Geographers and of the National Council of Geography Teachers. He had been president of the Faculty Science Club and of the local chapter of the North Carolina Education Association.

In the untimely death of Dr. Coy Phillips the Woman's College of the University of North Carolina has lost one of her most capable and loyal professors and the Academy has lost a devoted member.

ARCHIE D. SHAFTESBURY

MISS CORNELIA STRONG

On June 3, 1955, as the College was entering upon its commencement season, Miss Cornelia Strong, Professor Emeritus of Mathematics at the Woman's College of the University of North Carolina, passed quietly away. Although she

had been retired for seven years, she had maintained an active interest in the college affairs and its activities.

Miss Strong was a native of South Carolina and the daughter of a Presbyterian minister. She received her early education at the Agnes Scott Institute, not a standard four-year college at that time. After two years of teaching she entered Cornell University and in 1903 received her Bachelor of Arts degree and was elected to membership in Sigma Xi. It took real courage for this shy southern girl to go so far from home to the northland and to a coeducational institution; yet she always referred to her years there as very happy ones. Two lasting friendships with distinguished mathematicians developed during these days at Cornell: one with Professor John Henry Tanner and the other with Professor Louis Karpinski, later of the Mathematics Department of the University of Michigan. Several years after she had left Cornell, she returned to assist Professor Tanner in writing a high school algebra text. Two years after her graduation from Cornell she came to the Woman's College, then the State Normal School, and she remained an active member of its teaching staff for forty-three years.

Miss Strong attended summer schools at many universities: Cornell, Michigan, Harvard, California, Colorado and Wisconsin. It was from the University of Michigan in 1931 that she received her Master of Arts degree in Mathematics and Astronomy. Immediately thereafter she introduced courses in Astronomy at the college. But her interests extended beyond the subjects she taught and she often took courses in literature, poetry, government and sociology. She held memberships in a number of professional societies: the Mathematical Association of America, the North Carolina Education Association, the Astronomy Club of Greensboro, and she had been a member of the North Carolina Academy of Science since 1910.

Miss Strong's keen intellect and her ability to analyze a situation clearly, logically and without prejudice made her a most valuable member of the college faculty. Her associates were constantly impressed by the sharpness of her mind, her ability to discriminate and her clarity of expression. She was a member of many important committees, often serving as the chairman.

As a teacher, Miss Strong will be remembered by hundreds of alumnae who studied in her classes as a woman of profound knowledge and infinite patience, with concern and kindly interest always in the individual student.

To those in the Mathematics Department who worked intimately with her for so many years, she was the perfect colleague. Her co-operation was spontaneous even when she might feel hesitant about entering upon a new undertaking. The whole department gathered strength from her intellectual integrity and found delight in her keen sense of humor. The newer members of the department soon felt the warmth of her personality and learned to love and respect her. During the seven years after her retirement her advice was sought on many occasions and her judgment was always sound. She was an integral part of the department to the last.

In the hearts of her many students and friends, in the Mathematics Depart-

ment and in the entire Woman's College community, Miss Strong will live for many years to come, an inspiring and gracious influence.

HELEN BARTON

HELGE LUNDHOLM

Helge Lundholm, Professor of Psychology, and formerly Chairman of the Department of Psychology at Duke University, died on July 8, 1955 at the age of sixty-four. In his passing, the North Carolina Academy of Science suffered the loss of one of its distinguished members.

Professor Lundholm was born in Malmö, Sweden, on May 15, 1891. He received his early education in Sweden. His advanced studies in psychology and in the history of art were carried on at the University of Stockholm, with periods of study at Oxford, at Copenhagen, and at Paris where he spent a year in the study of painting and drawing. He received his doctorate from the University of Stockholm in 1919. In the same year, Professor Lundholm came to this country as a Fellow of the American Scandinavian Foundation for post-doctoral research in experimental aesthetics. From 1921 to 1930 he was a member of the psychological staff of the McLean Hospital, Waverly, Massachusetts, where he engaged in joint research on physiological concomitants of psychopathology. An interim of two years in Sweden was devoted to problems of industrial psychology, as Secretary of the Royal Institute of Industrial and Scientific Research. In 1930 Helge Lundholm came to Duke University as Associate Professor of Psychology. He became Professor of Psychology in 1937, and was Chairman of the Department of Psychology during the years 1939 to 1946.

Professor Lundholm joined the Department of Psychology at Duke University in the year in which the University expanded to the West Campus. Through his stimulating teaching, research and writing, and during the trying war years as Chairman of the Department, he contributed in a vital way to the course of its development.

Professor Lundholm's research and writing centered in the areas of aesthetics, psychopathology, and theoretical, systematic psychology. He was a productive scholar, publishing over forty articles in American, British and Scandinavian psychological and medical journals. His experimental studies of functional amnesia, hallucinations and of induced "laboratory neuroses" in human subjects were of high originality and theoretical relevance.

His main interest, as realized in six major monographs and books, was in the development of a conational theory of human nature genetically rooted in the traditions of British psychological thinking that had conditioned the work of his close friend, William McDougall. In an era characterized by a few dominating orthodoxies he stands out as one of the rare persons who had the courage to trust his own scientific imagination and to pursue the consequences of his own thinking fearlessly and with logical clarity. His career coincided with a period in which the subject matter of his science was becoming progressively dehumanized. In this atmosphere Lundholm's style of thinking showed an unusual sensitivity to the

relevance of experience of self and other specifically human phenomena to the foundation principles of the science.

A great reserve and dignity were characteristic both of his bearing and of his personal relations, and only a few close friends in addition to his early departmental colleagues were aware of the sympathy and kindness that lay underneath. Those who knew him well recognized and valued highly not only the significance of his professional contributions but also his more unusual qualities as a scientific thinker and as a human being.

KARL ZENER

SCIENCE EDUCATION IN N. C. HIGH SCHOOLS

The N. C. Academy, with the aid of other sponsoring agencies and individuals, has completed its second successful year in the new program of high school science fairs, essay contests and science talent search. The western region of the state was subdivided for district fair purposes with the result that fairs were held at Western Carolina College, Cullowhee and at Appalachian State Teachers College, Boone. This meant a total of seven district fairs and a state science fair held this year at the University of North Carolina, Chapel Hill. Essay contests in ornithology, forestry and wildlife were conducted at both district and state levels.

The essay contests and the science fairs were conducted by the High School Committee of the Academy with Dr. Hollis J. Rogers as chairman. Other leaders in this work were Dr. Victor A. Greulach, chairman of the State Science Fair held at the University of North Carolina on April 20 and 21, and the district fair chairmen as follows: Dr. J. O. Derrick, East Carolina College, Northeastern District; Dr. George W. Nace, Duke University, North Central District; Mr. D. H. Godbold, Wilmington City Schools, Southeastern District; Dr. Victor M. Cutter, Jr., Woman's College, U. N. C., North Piedmont District; Dr. H. E. Fulcher, Davidson College, South Piedmont District; Dr. Ray Derrick, Appalachian State Teachers College, Northwestern District; Professor J. G. Eller, Western Carolina College, Western District.

The Second North Carolina Science Talent Search was conducted by the following committee: Dr. B. B. Brandt, chairman, Dr. J. M. Clarkson and Mr. Henry Shannon. The North Carolina Search is correlated with the national Westinghouse Science Talent Search. There was an encouraging increase in the number of entries from high school seniors in North Carolina this year. William Happer of Lenoir High School won an honorable mention in the national contest, being one of 160 students over the nation so honored. Four students were named for honors in the N. C. Search: William Happer, Lenoir High School, Lenoir; Larry E. Klutz of Appalachian High School, Boone; Samuel Scott Stevens, Charles D. Owen High School, Swannanoa; and David K. Townes, Needham Broughton High School, Raleigh.

Two students, winning highest honors in the two divisions, Biological and Physical, of the State Science Fair, were sponsored in their trip to the National Science Fair held at Oklahoma City on May 11 and 12. The Academy, through

the courtesy of the Carolina Power and Light Company, provided the entrance fee for the two exhibitors, and their home communities provided travel expense. They were accompanied on the trip by their respective teachers, Miss Dorothy Wilson of Durham High School and Mr. Frank Eller of Myers Park High School, Charlotte. Charles Egerton of Durham High School entered in Biological Science and William Montgomery of Myers Park High School entered in Physical Science. All who have followed the development of the N. C. Science Fairs were highly pleased when word came that Charles Egerton had first place in the National Fair in the boys' division of Biological Science. On April 30–May 2, Charles had exhibited at the N. C. Medical Society state meeting at Pinehurst as a guest of that Society. As second place winners in the State Science Fair, Gladys Smith, Concord High School, Concord and Frank London, Durham High School, Durham were given honorary memberships in the AAAS for one year. These are offered through the courtesy of the AAAS.

Winners in the Forestry and Wildlife essay state contests have not been announced as yet but winners in the Ornithology essay contest are as follows:

Ornithology Essay Contest

"The Cardinal, Our State Bird"

First Prize: Betty Lou Wallace, Mountain Park High School, Mountain Park
(*Sponsored by Mr. and Mrs. E. O. Clarkson*)
Second Prize: Janet Binkley, Wake Forest High School, Wake Forest
(*Sponsored by Mr. and Mrs. Micou F. Browne in honor of her father, Dr. Z. P. Metcalf*)
Third Prize: Elizabeth Parkman, Waynesville High School, Waynesville
(*Sponsored by Mr. and Mrs. W. C. Mebane*)

Forestry Essay Contest

(*Sponsored by the North Carolina Forestry Association*)
"Forests and Our Way of Life"

Wildlife Essay Contest

(*Sponsored by the North Carolina Wildlife Federation*)
"The Importance of Water Resources to Wildlife"

STATE SCIENCE FAIR WINNERS

Biological Science

(*Sponsored jointly by the Carolina Biological Supply Company and Mr. J. D. Tayler of Denoyer-Goeppert Company*)

First Prize: Charles P. Egerton, Durham High School, Durham
Second Prize: Gladys Smith, Concord High School, Concord
Third Prize: Jean Wayland, Wake Forest High School, Wake Forest

Physical Science

(*Sponsored by Cardinal Products, Inc.*)

First Prize: William Montgomery, Myers Park High School, Charlotte
Second Prize: Frank London, Durham High School, Durham
Third Prize: Robert L. Smith, Albemarle High School, Albemarle

Mention should be made in this report of the numerous special gifts of money made during the past year to the High School Science program. In addition to those of sponsors mentioned in the reports on contests immediately above, gifts were made by the following: Westinghouse Meter Plant, Raleigh; Carolina Power and Light Company, Raleigh; N. C. Section, American Chemical Society; Central N. C. Section, American Chemical Society; Carolina Geological Society; Southern School Supply Company, Raleigh.

REPORT OF THE NOMINATING COMMITTEE

The committee, consisting of W. O. Puckett, J. L. Stuckey and Otto Stuhlman, submitted the following nominations:

President: Reinard Harkema, N. C. State College
Vice-President: J. F. Dashiell, U.N.C.
Member of Executive Committee: Maurice Whittinghill, U.N.C.
Member of Research Grants Committee: T. H. Eaton, East Carolina College

The above nominees were unanimously elected by the Academy. This concluded the business and the meeting was adjourned.

Approximately 125 members of the Academy, guests, and friends enjoyed the Annual Dinner of the Academy which was held in Lenoir Hall at 7 p.m. Vice-President Henry W. Jensen presided over the banquet and brief session immediately following. The 1955 Poteat Award was presented to Raymond L. Murray of N. C. State College for his paper in the Physics-Mathematics Section in 1955 titled, "The physics of nuclear reactors." Presentation of the 1956 John Bewley Derieux Memorial Award in physics was made by R. M. Helms of East Carolina College to William G. Dotson, a senior student at Wake Forest College. A feature of the session was the recognition of four winners in the Second North Carolina State Science Talent Search conducted by the Academy. Two representatives of the Westinghouse Meter Plant in Raleigh, Mr. Robert T. Cadwallader and Dr. Jules Medwin, presented the four high school seniors as honor guests of the Academy, and also presented them with personal gifts. Winners were William Happer of Lenoir High School, Lenoir; Larry E. Klutz of Appalachian High School, Boone; David Keith Townes, of Needham B. Broughton High School, Raleigh; and Samuel Scott Stevens of Charles D. Owen High School, Swannanoa. William Happer had previously won honorable mention in the national Westinghouse Science Talent Search. Only two teachers of these outstanding students were present to be presented. They were Mr. A. Maltbie of Needham B. Broughton High School, Raleigh and Mr. Kent Robinson of Appalachian High School, Boone. Brief remarks by President E. C. Cocke concluded the banquet session.

In place of the annual presidential address, the Academy members and friends

moved to Carroll Auditorium to hear an address on "Points of view in mathematics, their contrasts and connections" by Professor Heinz Hopf of the Swiss Federal School of Technology, Zurich. This address was jointly sponsored by the University of North Carolina chapter of Sigma Xi. Vice-President Henry W. Jensen presided. Following the lecture, all members and friends were entertained at a delightful social hour in the ballroom of the Carolina Inn as guests of the University of North Carolina.

The following officers were elected for the respective sections:

Biochemistry and Physiology: Chairman, F. G. Hall; Secretary, Claude Yarbro

Botany: Chairman, Jane Philpott; Secretary, L. A. Whitford

Geology: Chairman, J. M. Parker, III; Secretary, E. W. Berry

Mathematics: Chairman, Ivey C. Gentry; Secretary, Eleanor Jenkins

Physics: Chairman, William A. Parker; Secretary, R. M. Helms

Zoology: Chairman, Karl M. Wilbur; Secretary, Walter M. Kulash

The following constitute the personnel of the standing committees:

Executive: Reinard Harkema, J. F. Dashiell, John A. Yarbrough, C. S. Black, L. A. Whitford and Maurice Whittinghill

Research Grants: O. J. Thies, Maurice Whittinghill, H. J. Oosting, and T. H. Eaton

Dr. Reinard Harkema, President of the Academy for 1957, announced the appointment of the following committees:

Auditing: Arthur Kelman, G. Matrone, J. L. Allison

Nominating: E. C. Cocke, B. W. Wells, F. G. Hall

High School Science: H. J. Rogers, Mazel B. Lyke, Henry A. Shannon, Raymond C. Hatley, Claire Freeman

Conservation-Legislation: T. L. Quay, A. E. Radford, T. E. Maki, Wanda Hunter

Resolutions: Maurice Whittinghill

North Carolina Science Talent Search: B. B. Brandt, J. M. Clarkson, Henry A. Shannon

Representative on A.A.A.S. Council: John A. Yarbrough

Representatives to Academy Conference: J. F. Dashiell and John A. Yarbrough

The following papers were presented during the meetings. Those marked with an x are abstracted in these proceedings:

Guest Address: Points of view in mathematics, their contrasts and connections. Heinz Hopf, Swiss Federal School of Technology, Zurich

GENERAL SESSION

Recent advances in plant physiology. Aubrey W. Naylor, Department of Botany, Duke University

Advances in human genetics and their application to medicine. C. Nash Herndon, Bowman Gray School of Medicine

The science teaching improvement program. John R. Mayor, Director of Science Teaching Improvement Program, A.A.A.S., Washington, D. C.

BIOCHEMISTRY AND PHYSIOLOGY SECTION

x*A simplified gas analyzer for student use.* F. G. Hall and W. E. Hull, Duke University

x*The acetal phosphatide content of normal and atherosclerotic aorta tissue.* Bradford Miller and Carl E. Anderson, U. N. C.

The mechanism of formation of renal calculi. James C. Andrews and Claude L. Yarbro, U. N. C.

x*Evaluation of the precipitability test for saturation of urine with regard to calcium.* Claude L. Yarbro and John K. Haddad, U. N. C.

Excretory effects of diamox on water-loaded normal and adrenalectomized rats. Donald A. Olewine and Joseph H. Perlmutt, U. N. C.

Strontianite deposition in eggshells. Edwin M. Banks and Howard T. Odum, University of Illinois and Duke University

The mechanism of urea excretion in mammals. Bodil Schmidt-Nielsen, Duke University

A comparison of the diuretic effects of nitrate salts with other diuretic agents. Edwin P. Hiatt, U. N. C.

BOTANY SECTION

Some slime molds from North Carolina. T. W. Johnson, Jr., Duke University

Fungi—then and now. F. A. Wolf, Duke University

x*The effect of maleic hydrazide on the growth of some fungi.* Charles E. Miller and Victor A. Greulach, U. N. C.

Marine fungi from the Beaufort inlet. T. W. Johnson, Jr., Duke University

Some variations in Aphanodictyon papillatum *Huneycutt.* Thomas N. Johnson, Jr., Duke University

Host-parasite relationships of the lance nematode in cotton roots. L. R. Krusberg and J. N. Sasser, N. C. State

Comparative morphological studies on the soybean cyst nematode, Heterodera glycines *and the clover cyst nematode,* H. trifolii (Nematoda: Heteroderidae). Hedwig Hirschmann, N. C. State

x*Anthracnose of alfalfa in North Carolina.* J. L. Allison and G. A. Hemerick, N. C. State

Objectionable smoking quality in breeding lines of flue-cured tobacco. E. L. Moore and P. N. Drolsom, U. S. D. A. and N. C. State, Oxford

Root knot nematode resistance in tomatoes. W. S. Barham and J. N. Sasser, N. C. State

x*The current effect and growth of algae.* L. A. Whitford, N. C. State

Some effects of radioisotopes on the callus culture of Sequoia sempervirens. E. Ball, N. C. State

x*Effects of various combinations of day and night temperatures on growth of tree seedlings.* Paul J. Kramer, Duke University

x*The effects of certain environmental and chemical factors on heterophylly in* Armoracia aquatica. Graham J. Davis, U. N. C.

Blade tissue anatomy of foliage leaves of North Carolina shrub bog species. Jane Philpott, Duke University

The cell structure of Pylaiella fulvescens (*Schousb.*) *Born.* H. L. Bloomquist, Duke University

Chromosome studies on some North Carolina mosses. Lewis E. Anderson and Virginia S. Bryan, Duke University

x*Cytomixis in cotton.* Patricia Sarvella, N. C. State

x*Embryogeny of two species of cattail.* Philip E. Graef, E. Carolina College

x*The use of segregation ratios of synthetic allopolyploids as a taxonomic tool.* D. U. Gerstel, N. C. State

Comments on "The Wilderness World of John Muir." J. S. Holmes, Raleigh

x*A flora of the Carolinas.* H. R. Totten, U. N. C.

x*Distribution and speciation of the genus* Ludwigia *in North Carolina.* James A. Duke, Fort Detrick, Md.

A new hybrid oak from the piedmont of North Carolina. Lionel Melvin, Pleasant Garden. (Published in full in this issue of the Journal.)

x*A study of a colony of hybrid oaks.* Frances E. Silliman, U. N. C.

GEOLOGY SECTION

A marked alignment of earthquake epicenters in western North Carolina and its tectonic implication. G. R. MacCarthy, U. N. C. (Published in full in this issue of the Journal.)

x*The occurrence of fluoride in ground water in North Carolina.* H. E. LeGrand and P. M. Brown, U. S. G. S., Raleigh

x*Panama geology.* John M. Parker, III, N. C. State

x*Coal in Africa.* E. W. Berry, Duke University

The clay minerals of the North Carolina coastal plain formations. William D. Reves. U. N. C.

x*Some metasediments in the Grandfather Mountain fenster.* Mont J. Bright, Jr., U. N. C.

MATHEMATICS SECTION

The Lehmus-Steiner-Terquem problem: some new solutions. Archibald Henderson, U. N. C.

Deflection problems involving the integral of a product. T. F. Hickerson, U. N. C.

x*An interesting orthogonal transformation.* J. W. Lasley, Jr., U. N. C.

On the absolute greatest root of certain algebraic equations. Alfred Brauer, U. N. C.

PHYSICS SECTION

An introductory laboratory in modern physics. Joseph W. Straley, U. N. C.

A study of electric transformer phenomena. R. Marshall Helms, East Carolina College

Solid angle calculations by digital computers for radiation detectors. A. Victor Masket, U. N. C. (sponsored by Paul E. Shearin)

Some recent results on cosmic ray showers. Everett D. Palmatier, U. N. C.

Design of a gamma irradiation facility at the Raleigh Research Reactor. Charles Perrell and Clifford Beck, N. C. State

Magnetic properties as determined by neutron diffraction. Thomas J. Turner, Wake Forest

Experiments with positronium: Introduction by Arthur Menius. Messrs. Lundholm, Bjorkland, and Dough, N. C. State

Elementary theory of the excitation in liquid helium. O. K. Rice, U. N. C.

Several solid state experiments in progress at U.N.C. Lawrence Slifkin, U. N. C.

Activation analysis of water: Introduction by Clifford Beck. Dade Moeller, N. C. State

x*Perturbation integrals in nuclear reactor theory.* Gene A. Baraff, N. C. State

x*Fuel burnout effects in thermal reactors.* Arthur W. Banister, N. C. State

Discussion: Manpower shortage in physics. Introduced by William A. Parker, Catawba

ZOOLOGY SECTION

How a bee sees. W. A. Stephen, N.C. State

The life history and distribution of the carrot rust fly. H. Eldon Scott, N. C. State

x*Taxonomy of castes in social insects.* A. L. Pickens, Queens College

Studies on mating systems in Drosophila melanogaster. M. E. Jacobs, Duke University

Studies on a Drosophila *melanoma.* J. T. Bowman and M. E. Jacobs, Duke University

x*The restoration of egg production after a radiation-induced lapse in* Habrobracon (*Hymenoptera: Braconidae*). D. S. Grosch, N. C. State

Seasonal cycles in Silver Springs, Florida. Howard T. Odum, Duke University

x*An ecological study of caves, with especial reference to migrations.* J. D. Ives, Pinebluff, N. C.

Camels, heat, and water. Knut Schmidt-Nielsen, Duke University

Varieties, mating types and mating reaction in Paramecium bursaria. T. T. Chen, Duke University

Killer substances produced by Paramecium bursaria. T. T. Chen, Duke University

Three years of notes on the movements and hibernation of the woodchuck population of Jerico Mountain. Carl W. Galloway, Snow Hill, N. C.

The embryo of the angel shark, Squatina dumeril (*LeSueur*), *and notes on the species in North Carolina waters.* William E. Fahy, Institute of Fisheries Research, U. N. C.

An attempted analysis of the environmental control of seasonal reproduction in the marine snail, Nassa obsoleta. Charles E. Jenner, U. N. C.

x*A study of hybrid lethality in the sea urchin cross:* Lytechninus variegatus × Arbacia punctulata. H. E. Lehman and Lillian M. Youngs, U. N. C.

The generic concept for higher animals. Joseph R. Bailey, Duke University

x*A composite diagram of evolutionary changes.* T. H. Eaton, Jr., East Carolina College

x*The effects of immune sera prepared against their various components.* Edward C. Horn, Duke University

An electron microscope study of the growing surface of mollusc shell. Tadashi Tsujii, D. Gordon Sharp, and Karl M. Wilbur, Duke University

x*A method of transplanting tumor tissue directly to the lungs of mice.* Robert H. Tamis, Brookhaven National Laboratory and New York University College of Medicine

x*The influence of foreign epidermis on melanophore development in the salamander,* Triturus torosus. Lillian M. Youngs, U. N. C.

Developmental aspects of some teratoid parasites. W. C. George, U. N. C.

A Simplified Gas Analyser for Student Use. F. G. HALL AND W. E. HULL. There has been a need for a simple gas analyser for use in physiology classes for analyses of alveolar and other gases. The analyser demonstrated here was modified from the principle of the Scholander analyser. It consists of a gas burette, sampler and appropriate gas absorbing reagents. It is particularly suitable for analyses of carbon dioxide and oxygen. Analyses can be made in two to three minutes, and with adequate accuracy for class work. The advantages are that there are no stopcocks and little time is consumed in acquiring technique.

The Acetal Phosphatide Content of Normal and Atherosclerotic Aorta Tissue. BRADFORD MILLER AND CARL E. ANDERSON. A preliminary study has been made of the content of acetal phosphatides in the lipids of normal and atherosclerotic aortas. Removed from the adventitia, the combined intimal and medial layers from normal tissue areas and graded atherosclerotic plaques were dried *in vacuo* in the cold, weighed, pulverized and extracted with hot 1:1 acetone-methanol. The solvent was filtered off and the residue analyzed for non-lipid nitrogen by the macro-Kjeldahl procedure. The acetone-methanol extracts were evaporated to dryness and the residue taken up in 30–60° petroleum ether from which aliquots were taken for total lipid determination by evaporation to dryness and weighing the residue. Total lipid phosphorus was determined by the Fiske-Subbarow method after wet ashing, and acetal phosphatides by Yarbro's modification of the Feulgen-Andresen-Bolguth procedure. On a dry weight basis, non-lipid tissue residue nitrogen decreases with an increasing degree of calcification. Total lipids and total phospholipids increase with increasing severity of involvement while the concentration of acetal phosphatides decreases. The same direction of change for total lipid, phospholipid and acetal phosphatide was noted when non-lipid tissue residue nitrogen was used as a basis for comparison, except that the decrease in acetal phosphatides was not as large. At present a study of the changes, with increasing severity of the disease, of components of the phospholipid fraction is in progress.

*Evaluation of the Precipitability Test for Saturation of Urine with Regard to Calcium.** CLAUDE L. YARBRO AND JOHN K. HADDAD. The mechanism of urinary calculus formation is not very well understood. Many factors, among them supersaturation of the urine with regard to calcium phosphate or oxalate, have been

* Supported by a grant (A-248) from the National Institute of Arthritis and Metabolic Diseases of the National Institutes of Health, Public Health Service.

suggested by various investigators. Flocks, (*Jour. Urol.* **65,** 721, 1941) designed a test to indicate susceptibility to urinary calculus formation. This test consisted of shaking 100 ml. of urine with one gram of tertiary calcium phosphate for ten minutes. Whether calcium dissolved or precipitated under these conditions was taken as an indication of under- or supersaturation of the urine with respect to calcium. Recently Culp and Flocks (*Jour. Urol.* **73,** 938, 1955) noted a wide variation in the calcium precipitability in the urine from the same patient from day to day.

In an effort to evaluate Flocks' procedure both urine and water which had been previously saturated with secondary calcium phosphate were equilibrated with calcium oxalate or tertiary calcium phosphate in a mechanical shaker over a 48-hour period. The concentration of calcium and/or phosphate in the urine or water solution was followed at various intervals of time during the equilibration. The effects of varying the amount of solid phase and the particle size of the solid phase were investigated under these conditions. The results obtained indicate that a 10-minute equilibration period is not sufficient to saturate either urine or water with the more insoluble calcium salts. However, saturation is approached with a 6–12-hour equilibration time. The equilibration curves obtained indicate that during the first two hours changes are occurring at their most rapid rate and do not necessarily reflect the true conditions of under-/or supersaturation. The rates of these changes are influenced by both the particle size and the amount of solid phase. In general, the larger amounts of solid phase, or the smaller particle size of the solid phase produced more rapid changes. These data indicate that Flocks' precipitability test is not a true reflection of under-/or supersaturation of urine with respect to calcium, and therefore necessitate a re-evaluation of his test.

The Effect of Maleic Hydrazide on the Growth of Some Fungi. CHARLES E. MILLER AND VICTOR A. GREULACH. Twenty-two species of fungi were cultured in petri dishes on agar incorporating a yeast extract medium buffered to pH 6.8 by means of phosphate buffers, and with 0, 2000 and 5000 p.p.m. maleic hydrazide added to the culture medium. The various species differed in their reactions to MH, ranging from *Pythium sp.*, which with 5000 p.p.m. MH grew only 7.9 per cent as much as the controls, to *Sordaria fimicola*, which had 162.9 per cent of the growth of the controls when 5000 p.p.m. MH was used. The species studied can be classed in two main groups: those which are inhibited to a greater or lesser degree by MH and those which are not. Some of the species in the second group are apparently able to utilize MH, probably as a nitrogen source, while others are not.

Anthracnose of Alfalfa in North Carolina. J. L. ALLISON AND GLENN A. HEMERICK. The increased acreage of alfalfa in North Carolina has been accompanied by the build-up of several destructive fungus diseases of this crop. One of these is anthracnose caused by *Colletotrichum trifolii* Bain and Essary. Anthracnose is most prevalent and destructive during the late summer and early fall months in warm wet periods. Four distinct symptoms are induced, (1) damping-off of seedlings, (2) petiole blight, (3) stem lesions and (4) girdling. Girdling is

followed by wilting and death of foliage and is the dominant symptom in older established stands of alfalfa. The reproductive cycle of the fungus is about 100 hours at 75°F. The fungus produces scattered masses of hyaline conidia in raised acervuli sparsely bordered with dark setae. Conidia are bluntly pointed at the base, rounded at the apical end and are approximately 5 × 15 microns in size. In inoculation tests, alfalfa was found to be very susceptible and red and white clovers less susceptible to 10 different single conidial isolates of the fungus. Among 20 named varieties of alfalfa tested none were consistently resistant to the fungus, although resistant plants did occur in all varieties. Selection and breeding for anthracnose resistance in alfalfa is the only practical means of control, and work in this direction is under way.

The Current Effect and Growth of Fresh-Water Algae. L. A. WHITFORD. The importance of a current of water to attached organisms living within it is sometimes recognized by ecologists and limnologists but rarely explained. A current increases the diffusion gradient by maintaining the concentration of inwardly diffusing materials near a plant surface and sweeping away the products of metabolic activity. Both observations and experimental data seem to indicate that fresh-water algae and higher plants can grow in running waters at higher temperatures and under other conditions which would make growth impossible in still water.

In *Phaeosphaera perforata*, a species growing in brooks, more rapid cell division at the surface of a colony may produce first a hollow cylinder and later an expanded perforate colony. This may result from the current effect on the growth of surface cells.

Effects of Various Combinations of Day and Night Temperatures on Growth of Tree Seedlings. PAUL J. KRAMER. Although it is generally assumed that temperature has important effects on tree growth, few data are available concerning the optimum temperature for the growth of any species or the effects of various combinations of day and night temperatures. In order to obtain quantitative data, tree seedlings of several species were grown at various temperatures in the air-conditioned greenhouses of the California Institute of Technology. The day temperatures used were 17°, 23° and 30°C.; the night temperatures were 11°, 17° and 23°C. The day temperatures were maintained for 8 hrs., the night temperatures for 16 hrs. Natural illumination and natural photoperiod were used for the experiments reported here. The seedlings were grown in quart containers in a mixture of crushed rock and vermiculite and were watered with deionized water and nutrient solution at regular intervals. Growth in height was measured weekly from February 17 to the end of October.

The results showed clearly that high day temperatures resulted in increased growth, but high night temperatures caused decreased growth. A day temperature of 17°C. was much too cool for good growth and night temperatures as high as day temperatures were very unfavorable for growth. Best growth was obtained with night temperatures 12 or 13 degrees lower than day temperatures. The highest temperature used resulted in most rapid growth early in the season, but poor growth in the latter part of the season and early cessation of growth. Al-

though trees subjected to low temperatures were slow to resume growth in the spring they tended to grow later in the autumn than trees at higher temperatures.

It seems that the relation between day and night temperatures has important effects on the growth of both species. It appears possible that the relative levels of day and night temperatures may be a factor in controlling the length of growing season and in limiting the southward extension of northern tree species.

The Effects of Certain Environmental and Chemical Factors on Heterophylly in Armoracia aquatica. GRAHAM J. DAVIS. Cuttings of the amphibious crucifer, *Armoracia aquatica* (Eat.) Wieg., were raised indoors under various photoperiods, light intensities, and temperatures in order to determine the effects of these factors on leaf shape. Plants which grew terrestrially on 10-, 12-, 13-, 14-, and 24-hour photoperiods at 200 ft-c. produced leaves with few or no lobes in the experiments in which the mean daily temperature was 25.4°C. or higher. When the mean daily temperature was less than 25.4°C., the leaves formed were divided or highly lobed regardless of the photoperiod variations. Interruption of the middle of the dark period with an hour of light when the photoperiod was 10 or 12 hours, and variations in light intensity (100, 200, and 250 ft-c.), had no effect on the amount of lobing. Plants were also maintained under approximately 8 cm. of water. Temperature was the controlling factor here too, with entire leaves being produced at the higher ranges.

Treatment of the plants with various combinations and concentrations of indole-3-acetic acid, 2,3,5-tri-iodobenzoic acid, adenine sulfate, and 2,6-diaminopurine resulted in some changes in leaf development; but the evidence is not such that any general conclusions can be drawn as to the internal factors controlling heterophyllous development.

Cytomixis in Cotton. PATRICIA SARVELLA. Cytomixis, the extrusion of chromatin from one cell into another, was observed in both squashes and sections of cotton pollen mother cells and in both pure species and interspecific hybrids. This process was seen mostly in late meiotic prophase but was observed as late as telophase II. The chromatin moved through wide cytoplasmic bands connecting the pollen mother cells. At metaphase, binucleate cells and cells with deficient or abnormally high chromosome numbers were observed. These cells were thought to be the results of cytomixis, and may be taken as evidence that cytomixis is not merely an artifact. During mitosis, loss of chromosomes may also be an expression of cytomixis. Incomplete wall formation, leaving cytoplasmic bands between the pollen mother cells, was thought to be responsible for cytomixis.

Embryogeny of Two Species of Cattail. PHILIP E. GRAEF. The present investigation attempts to trace the development of the embryos of *Typha latifolia* and *Typha angustifolia*. The term *proembryo* is used to designate all stages of embryogeny prior to the appearance on one side of the proembryo of a depression which indicates the point of origin of the shoot apex, and the term *embryo* to all stages of ontogeny from the appearance of this notch to the mature embryo.

The zygote begins its development into the proembryo after the endosperm nucleus begins active division. After the elongate proembryo has developed into an embryo, by the appearance on one side of a depression in which the shoot

apex makes its appearance, the free-nucleated endosperm becomes cellular and starch grains form in the endosperm cells. The upper part of the embryo develops rapidly to form a long, straight cotyledon while the lower part of the embryo forms the short epicotyl-hypocotyl-radicle axis. The histogens, including a distinct calyptrogen, are differentiated in the apex of the hypocotyl-radicle axis. The axial core of the embryo gives rise to the procambium. That portion of the embryo between the procambium and the embryonic covering layer forms the embryonic cortex. The cells of the cotyledonary embryonic cortex become filled with starch grains. The mature straight embryo occupies the entire length of the seed and its cotyledon is approximately four times the length of the rest of the embryo.

The present study therefore reveals that the embryos of the two species investigated follow the Onagrad type of embryogeny.

The Use of Segregation Ratios of Synthetic Allopolyploids as a Taxonomic Tool. D. U. GERSTEL.* Studies of comparative chromosome morphology and pairing behavior in hybrids have in the past been used for the elucidation of some taxonomic problems. Preferential pairing in allopolyploids has been little considered in this connection. Yet, in the genus *Gossypium* at least, the degree of preferential association between homologous chromosomes of the parent species in synthetic allopolyploids follows taxonomic relationships. Thus, amphiploids from closely related *G. arboreum* and *G. herbaceum* showed random tetrasomic segregation, producing a 5:1 gametic ratio (5 loci tested). In contrast, amphiploids between Old World cotton species and distant *G. anomalum* were almost stable (5 loci). Other combinations produced ratios between these two extremes. The gametic output from *G. hirsutum-raimondii* amphiploids varied between 8.3:1 and 12:1 (5 loci) while that from *G. hirsutum-thurberi* gave much wider ratios ranging from 24.3:1 to 47.0:1 (2 loci). The last-mentioned results provide new evidence for Stephens' view based on morphogenetic evidence that *G. raimondii* is taxonomically closer to *G. hirsutum* than *G. thurberi*.

A Flora of the Carolinas. H. R. TOTTEN. Five staff members (J. E. Adams, H. E. Ahles, C. R. Bell, A. E. Radford and H. R. Totten) of the Department of Botany of the University of North Carolina at Chapel Hill, have begun the work of compiling a Flora of the Carolinas. The published work will name and describe every species of vascular cryptogam and seed plant in our area. With keys for identification, detailed distributional data, ecological notes, and clear illustrations, it will be an indispensable tool for the practicing biologist as well as an authoritative guide for the layman interested in plants.

The biologists of our area are cordially invited to have an active part in making a concrete scientific contribution to this important research project, by undertaking to make plant collections in their respective counties. Every adequately labelled specimen sent to Chapel Hill will receive the attention of a specialist. For certain critical groups we are receiving assurance of the aid of collaborators who are experts in those fields.

A Study of a Colony of Hybrid Oaks. FRANCES E. SILLIMAN. A colony of hybrid

* Supported by a grant (G720) from the National Science Foundation.

oaks which represent crosses between *Quercus alba*, the white oak, and *Quercus prinus*, the rock-chestnut oak, was studied. The population analysis was made with the aid of Anderson's hybrid index method. Index values were assigned to six vegetative characteristics considered to be distinctive in separating the parental species and a scatter diagram was constructed from the results. It has been concluded that approximately 3 per cent of the population are members of the F_1 generation and approximately 37 per cent constitute F_2 segregates or represent back-crosses with the chestnut oak parent.

Distribution and Speciation of the Genus Ludwigia *in North Carolina.* JAMES A. DUKE. The fifteen species of *Ludwigia* found in North Carolina are categorically divided into four sections: two alternate-leaved and two opposite-leaved. Inherent in the alternate- and opposite-leaved species are similar reduction tendencies. Four distributional patterns are rather clearly defined. The genus is complicated by varietal and specific intergradations, and probably by hybridization.

The Occurrence of Fluoride in Ground Water in North Carolina. H. E. LEGRAND AND P. M. BROWN. According to medical research, a concentration of 1 part per million of fluoride in water used for drinking and cooking is sufficient to lessen the incidence of dental caries in children, but a concentration of more than 1 p.p.m. may cause mottling of teeth. In view of the importance of this chemical constituent in drinking water, studies are being made of the occurrence of fluoride in ground water in North Carolina as part of the investigations in cooperation with the North Carolina Division of Mineral Resources. Water containing more than 1 p.p.m. of fluoride in North Carolina is rare except in some deep wells in some northeastern counties, mainly in Gates, Bertie, Martin, Hertford, Chowan, Beaufort, and Pitt counties Water from wells shallower than 100 feet in North Carolina contains no appreciable concentrations of fluoride.

The causes of the varying distribution of fluoride in natural waters have not been established. Fluoride in water of the Coastal Plain of North Carolina is not confined to a single geologic formation and is not the result of any single factor. However, the greatest concentration of fluoride in water occurs under the following collective conditions: (1) in beds older than middle Eocene, (2) with increasing depth, (3) in beds having significant amounts of glauconite, (4) in water of high bicarbonate content, chiefly sodium rather than calcium bicarbonate, and (5) in beds from which connate artesian water has been flushed most recently. In places where one or more of the above conditions is not present, some waters have low concentrations and others have high concentrations of fluoride; consequently, no one of the conditions can be exclusively responsible for the presence of fluoride in solution.

In the laboratory, distilled water was repeatedly passed separately through samples of glauconitic sand, phosphatic sand, and shell marl, representing three of the aquifers of the Coastal Plain. The concentration of fluoride was nearly the same from each type of material, but from each type the final concentration of fluoride in solution was less than that during some prior time in the laboratory test. Although the complete significance of this fact is not known, the tests, as well as field studies, suggest that the amount of fluoride in ground water is not

directly proportional to the concentration of fluoride in rocks from which the water is withdrawn or through which it passes.

Study of the chemical changes in moving natural water, especially of the behavior of ions in the process of natural dilution of connate artesian water by fresh-water recharge, may throw light on the distribution of fluoride in ground water.

Panama Geology. JOHN M. PARKER, III. Topographic and geologic features in and adjacent to the Panama Canal Zone trend generally northeast. Bedrock units fall into four groups: (1) pre-Cenozoic metamorphosed volcanic rocks; (2) Cenozoic marine sediments (sandstones, shales, limestone, and muck, in part tuffaceous); (3) Oligocene and Miocene mafic lava flows; and (4) Miocene mafic plugs and dikes. High-angle faults divide these rocks into scores of small and large irregular blocks. Differential vertical and horizontal displacements have resulted in a complex mosaic. Topographic forms are controlled mainly by rapid stream dissection of semi-consolidated rocks following geologically recent differential uplift and subsidence of the fault blocks.

Coal in Africa. E. WILLARD BERRY. Coal of Carboniferous age is mined in Algiers. Permian coal is mined in the Belgium Congo. Coal is mined from the Ecca Series (Permo-Triassic) in the following districts: Wankie, Southern Rhodesia; Witbank and Natal in Union of South Africa; Mozambique; Madagascar; and in the Niger Valley. I have a sample of coal from the Soudan (it appears to be only a carbonized log) age unknown. These coals range in thickness from a few inches up to 35 or 40 feet. In general, ash content is high. Coking coals occur but often coals must be blended to coke. The Union of South Africa is processing coal for gasoline.

Some Metasediments in the Grandfather Mountain Fenster. MONT J. BRIGHT, JR. The Grandfather Mountain fenster north of Blowing Rock, N. C., contains metamorphosed sedimentary and igneous rocks. The rock series includes Upper Precambrian gneiss, schist, granite, rhyolite, greenstone and Lower Cambrian quartzite, conglomerate and slate. In the area covered by this report, the rocks have a fairly constant schistosity, generally striking N. E. and dipping S. E. Folds vary in size from microscopic to hundreds of feet in width, and usually plunge in a southerly direction. All formations are jointed, and little fracture cleavage is found. With respect to economic geology, the area is of little value, although mentionable quantities of roadmetal and building stone do occur.

An Interesting Orthogonal Transformation. JOHN W. LASLEY, JR. A conic, not a proper parabola, has at least one center. A translation to a center keeps the second degree terms invariant and removes the linear terms. A translation to any one of the centers, if multiple, effects the same result. A rotation then removes the product term, putting the equation in the form of a modified sum of squares.

It turns out that a single orthogonal transformation will also reduce the conic, if not a proper parabola, to this same simple (canonical) form. By means of this transformation and associated invariants, we can show that a conic is a pair of real lines, a repeated line, a pair of conjugate complex lines, according to whether the trace of the adjoint matrix of the conic is negative, zero or positive.

We thus have three criteria to distinguish between degenerate conics. The

rank tells of distinctness, without regard to reality. The discriminant tells the kind (parabolic, elliptic, hyperbolic) of conic from which our lines degenerate. The trace distinguishes distinctness: by being not zero, if distinct; zero, if not distinct. It distinguishes reality by being positive for real lines and negative for complex ones.

Perturbation Integrals in Nuclear Reactor Theory. GENE A. BARAFF. When a nuclear reactor which is running at constant power is perturbed by slight changes in its composition such as fuel burnout, or addition of local scattering or absorbing materials, the flux becomes time dependent and rises or falls like $e^{\omega t}$. Perturbation theory furnishes an approximate expression for ω which is

$$\omega = \frac{\int \Psi P \Phi \, dv}{\int \Psi \Phi \, dv}$$

In one group theory, Ψ and Φ are both the actual flux and P is an operator which corresponds to the changes in the constants in the reactor diffusion equation. In the two group theory, this P operator may be represented by a matrix operator P. Φ is $\begin{pmatrix}\phi_1\\ \phi_2\end{pmatrix}$ where ϕ_1 is the fast flux, ϕ_2 is the slow flux, and Ψ is (ψ_1, ψ_2) where ψ_1 and ψ_2 are functions related to the actual fluxes.

It has been found that $\psi_1\psi_2\phi_1\phi_2$ are linear combinations of two functions which may be denoted by ξ_1 and ξ_2. The form of ξ_1 and ξ_2 is dependent on the region in the reactor. But one can introduce matrices of constants, different for each region so that Ψ and Φ can be written

$$\Phi = \begin{pmatrix}\phi_1\\ \phi_2\end{pmatrix} = \begin{pmatrix}G_{11} & G_{12}\\ G_{21} & G_{22}\end{pmatrix}\begin{pmatrix}\xi_1\\ \xi_2\end{pmatrix} = G\xi$$

$$\Psi = (\psi_1, \psi_2) = (\xi_1, \xi_2)\begin{pmatrix}F_{11} & F_{12}\\ F_{21} & F_{22}\end{pmatrix} = \xi^+ F$$

then

$$\omega = \frac{\int \xi^+ FPG\xi \, dv}{\int \xi^+ FG\xi \, dv}$$

Suitable transformation of the upper integral replaces the matrix P which contains differential operators by the matrices N and O which contain only numbers in such a way that the expression for ω can be given by

$$w = \frac{\int \nabla\xi^+ FOG\nabla\xi \, dv}{\int \xi^+ FG\xi \, dv} + \frac{\int \xi^+ FNG\xi \, dv}{\int \xi^+ FG\xi \, dv}$$

The advantage of this notation is that for the most important perturbations, the elements of N and O are either constant in a given region and vanish outside it, or are combinations of constants and the functions $\xi_1\xi_2$. Thus these constants may be removed from the integration sign, and only integrals involving products of the functions and their gradients need be evaluated.

Values of the elements of F and G have been prepared for the three most used reactor geometries, and extensive tables of the integrals of the type involving products of these ξ functions and their gradients have been compiled for the above three geometries. Use of the perturbation theory is thus reduced to arithmetic evaluation of certain expressions and the combination of these with certain constants.

Fuel Burnout Effects in Thermal Reactors. ARTHUR W. BANISTER. The diffusion equation for neutron motion in a homogeneous reactor may be written as follows:

$$D\nabla^2\phi - \Sigma_a\phi + S = 0$$

In the simple case of a one group reactor, S becomes $K\Sigma_a\phi$.

If one assumes a uranium burnout proportional to ϕ, coupled with a uniform withdrawal of poison to keep the reactor critical, the perturbed equation is obtained:

$$D\nabla^2\phi - \phi(\Sigma_a - \Delta\Sigma_u - \Delta\Sigma_p) + \eta(\Sigma_u - \Delta\Sigma_u)\phi = 0$$

The solution to this equation is obtained by transposing the perturbed elements to the right side, approximating them with functions appropriate to the geometry, and obtaining complementary and particular solutions. The critical relation between $\Delta\Sigma_p$ and $\Delta\Sigma_u$ is then obtained by applying boundary conditions to the perturbed flux.

This method has been extended to the modified one-group, age-diffusion, and two-group cases, with and without reflector. Fission product buildup effects can also be included, either simultaneously or separately. Results are most easily obtained in the slab geometry, although other shapes can be handled. The assumptions made are valid for all reactors using highly enriched fuel (20% or greater).

Taxonomy of Castes in Social Insects. A. L. PICKENS. The "tree-diagram" so often used in graphing the taxonomic relation of organic forms has proved unsatisfactory in showing caste relations. Common insects hatch from the egg and develop to reproductive adulthood as if along a Gothic I. Bees, as reproductives and workers, seem to follow a V. Ants develop from the egg-mass as if along the bars of a Y with intermediate forms between the workers and soldiers. Termites show so many intermediate forms, even worker-reproductives and soldier-reproductives, that it is suggested that they appear to follow the spokes of a wheel radiating as if from a hub. Interblendings as in the artist's color-wheel, and maturity attained in different instars, make for numerous castes, intercastes and subcastes. Species showing nasutes instead of regular soldiers offer a challenge to tropical investigators in determining how this unusual form arose—perhaps from

the soldier, which it replaced—and what intermediate vestigial examples may or may not be expected to occur in such social groups.

The Restoration of Egg Production after a Radiation-Induced Lapse in Habrobracon (*Hymenoptera: Braconidae*). DANIEL S. GROSCH.* Fractionation of the permanently-sterilizing X-ray dose or a decrease in the intensity of irradiation allows recovery in the sense that some eggs are laid after a short period of temporary sterility. Temperatures above 20°C. promote recovery. Above 30°C. the phenomenon is much enhanced quantitatively. On the other hand, no restoration is observed if the wasps are held at 0°C. between fractions. Thus only at temperatures low enough to inhibit metabolism are X-ray doses (separated in time) found additive.

Experiments on chromosomal aberrations induced in plants suggest a cytological basis for the phenomenon. Recent observations on freshly isolated human ova show that the histological unit of nurse-cells-oocyte is not limited merely to arthropods. Such information from other laboratories gives promise of wider applications of insect sterility studies than hitherto realized.

An Ecological Study of Caves, with Especial Reference to Migrations. JOHN DUNBAR IVES. A historical review of cave study, from a biological point of view, was considered. Light, temperature and relative humidity were stated as the ecological factors mostly used. However, the evaporating power of the air, air currents, the pH, and the oxygen content of the water were also considered. In one cave a complete chemical analysis of the water of the cave stream had been made.

The cave animals were classified as (1) twilight inhabitants and (2) those living in total darkness. A tabulation of the light relationship of animals found in Mammoth Cave, Ky., Wyandotte Cave, Ind., Indian Cave, Tenn., and several other Tennessee caves was given.

In the cave studied especially for migrations, the inward migration, in the fall, of both the Thysanuran, *Machilis variabilis*, and the camel cricket, *Ceuthophilus ensifer*, took place during a period of outward diminishing light, temperature and relative humidity. The outward migration from the cave in the spring took place during a time of nearly constant relative humidity in the twilight region of the cave, increasing light and temperature, probably with increased metabolism and a desire for food in both the Thysanuran and the cricket.

The outward migration, from the deep interior, of *Amoebaleria defessa* took place during a time of diminishing light, in the entrance regions, and increasing temperature and relative humidity. These changes in the spring tend to make the entrance region comparable with the deep interior. The return migration, from the entrance regions to the deep interior, occurred during increasing light and temperature and diminishing relative humidity, conditions which are less comparable with those of the deep interior which is the natural habitat of this species.

* These investigations were supported by the U. S. Atomic Energy Commission. We are indebted to Dr. T. C. Worth and his Rex Hospital assistants (Raleigh) for X-ray exposures.

A Study of Hybrid Lethality in the Sea Urchin Cross, Lytechinus variegatus ♀ × Arbacia punctulata ♂. H. E. LEHMAN AND LILLIAN M. YOUNGS. Successful crosses were obtained by treatment of *Lytechinus* eggs for two hours with *Arbacia* "egg water," followed by an additional treatment of the eggs for 3–5 minutes in alkaline sea water, pH 9.3–9.6, and inseminating heavily in the alkaline sea water. The highest percentage of fertilization obtained in 18 attempts was 29%; most runs yielded less than 1% activation, which was determined by fertilization membrane elevation. Most activated eggs cleaved regularly and developed into swimming blastulae. The majority of blastulae failed to gastrulate or were arrested as abnormal mid-gastrulae. A few cases developed to plutei and the skeletons of these hybrid larvae exhibited both maternal and paternal characters. However, the individual cases that were most normal in body form possessed predominantly maternal-type skeletons. It is suggested that lethality in this cross resulted from incompatibility of *Arbacia* nuclear material with *Lytechinus* cytoplasm in post-blastula development, and that the few postgastrulae obtained represented cases in which paternal (*Arbacia*) chromatin had been to a large extent eliminated from the division figure during early cleavages.

A Composite Diagram of Evolutionary Changes. THEODORE H. EATON, JR. After obtaining clear-cut data on phylogenetic changes in several (up to 6 or 8) characters present in a given taxonomic group of animals, it is possible to represent these changes in a simple manner, as a composite phylogenetic tree. The position of primitive, advanced, or divergent branches is indicated in the usual way, but each part of the tree itself consists of parallel lines, one line for each evolving character. The primitive condition of each character may be shown by a solid line, which then continues as a broken line when some progressive change takes place, and still further change may be indicated by dotting the line, ad lib. Therefore the number of solid, broken, or dotted lines in any part of the tree serves as a measure of the extent of change which has taken place up to that part of the tree, so far as the given characters are concerned. Facts regarding each line and its meaning may be presented as a legend under the figure, or by key numbers.

*The Effects of Immune Sera Prepared Against Their Various Components.** EDWARD C. HORN AND MARY ELIZABETH HOUSE. Rabbit antisera have been prepared against washed, whole Ehrlich ascites tumor cells of mice and against nucleoprotein, nuclei, and mitochondria-microsome fractions of these same cells. In addition, mouse liver homogenate, mouse ascitic fluid, and bovine plasma albumin have been used antigenically to obtain for comparative purposes rabbit antisera of a heterologous nature.

The titers of these antisera were obtained in three ways: (1) by measuring their ability at different dilutions to agglutinate an ascites cell suspension of constant concentration; (2) by measuring their ability at different dilutions to fix complement in the presence of homologous and heterologous antigens; and (3)

* This work was supported in part by a research grant (RG-4203(C) from the National Institutes of Health, Public Health Service.

by determining their effects on ascites cells *in vitro* through a study of survival of mice injected with the treated cells.

Agglutination of cell suspensions showed the anticell serum to have the highest titer by far, as would probably be expected. The CF titers were less discriminating than agglutination although cell-anticell, mitochondria-antimitochondria, mitochondria-antinuclei, and nuclei-antimitochondria reactions showed somewhat higher titers than other combinations tested. The *in vitro* incubation of cells with all antisera, their subsequent testing for a reaction by injection into mice, and study of the latter's survival revealed the antimitochondria and antinuclei sera to be the only two which were cytotoxic.

The three tests employed then must be measuring qualitative as well as quantitative differences among the antisera. There seems to be little or no relationship between the mechanisms of agglutination and CF on the one hand and cytotoxicity on the other.

*A Method of Transplanting Tumor Tissue Directly to the Lungs of Mice.** ROBERT HOWARD TAMIS. The increased incidence of bronchogenic carcinoma in humans has made it desirable to develop pulmonary tumors in experimental animals that simulate, in certain respects, those occuring in man. These could then be used in a variety of studies, in an effort to learn more of the behavior of such tumors in animals, and its possible application to human pulmonary neoplasms.

Several different methods of approaching the lungs were used in an attempt to grow an anaplastic malignant tumor of mouse brain origin in the lungs of mice. The tumor was aseptically removed, ground in a mortar and pestle, and then suspended in saline. The intravenous, intrathoracic, intratracheal, and intrabronchial methods were proved unsatisfactory because of high mortality rates, multiple foci of tumor growth in various sites, or the time involved in the operations.

An inhalation technique was found to be a satisfactory method for growing transplantable tumor specifically in the lung. Of 125 mice used in this group, 25 developed tumor, and 24 of these were restricted solely to the lung, as determined by autopsy. This method is rapid (15 mice per hour), easy, and carries a low mortality rate (4 per cent).

The Influence of Foreign Epidermis on Melanophore Development in the Salamander, Triturus torosus. LILLIAN M. YOUNGS. In *Triturus torosus* a local increase in melanophores is obtained by grafting epidermis from several species of *Amblystoma* to the flanks of *torosus* hosts. To test whether the increment in pigment cells under the foreign epidermis is due to the differentiation of additional melanophores, or to the redistribution of the normal complement of *torosus* pigment cells, the following experiments were performed. At embryonic stage 25–27, ten grafts of skin ectoderm for each of three species of *Amblystoma* (*A. tigrinum*, *A. punctatum*, *A. mexicanum*) were placed on the right flank of stage 25–27 *torosus* hosts. The melanophores which differentiated on the right (graft) and left (non-graft or control) sides of these hosts were counted and averaged for the ten animals comprising each of the three experimental series. The data obtained

* This work was supported by the Atomic Energy Commission.

indicated clearly that, although a much greater concentration of melanophores was present under the foreign epidermis, the total number of pigment cells on graft and control sides of the *torosus* hosts remained approximately equal. Furthermore, the increase in melanophores under the grafted epidermis was accompanied by reductions in the number of pigment cells in areas adjacent to the graft. It was concluded that the increase in melanophores under the foreign epidermis was due to the redistribution of the normal complement of host melanophores. Since Twitty (Jour. Exp. Zool. **100:** 141–178, 1945) demonstrated that *torosus* melanophores will aggregate in any region that tends to accelerate pigment synthesis, it was suggested that the increment and retention of melanophores under the foreign epidermis is an expression of this characteristic.

PROCEEDINGS OF THE ELISHA MITCHELL SCIENTIFIC SOCIETY

1955–56

522ND MEETING, OCTOBER 11, 1955

J. C. MORROW (Chemistry): *Rotation in Solid Methane.* The gradual transition in solid methane at 20.4°K is characterized as an order-disorder transition. The fact that there are two orientations of the methane tetrahedra with nearly equivalent energies leads to prediction of R1n2 = 1.38 cal. deg.$^{-1}$ mole^{-1} for the entropy of the transition. Excess entropies of transition calculated from specific heat data accumulated by Clusuis and co-workers are 1.1 (CH_4), 1.3 (CH_3D), 1.3 (CD_4). The methane transition is like those observed for the ammonium halides and alkali borohydrides.

The non-lattice heat capacity difference for CH_4 and CD_4 can be represented by the difference of two Einstein functions with frequencies standing in the ratio $2^{\frac{1}{2}}$:1. A Debye-Einstein analysis for the individual heat capacity curves fails because of the gradual change from torsional oscillation to rotation at temperatures above the lambda point. At the melting point, C_p for CH_4 is 10.3 cal. deg.$^{-1}$ mole^{-1}; (3/2)R (for free rotation) plus the lattice heat capacity is 8.8 cal. deg.$^{-1}$ mole^{-1}. The difference between those values is of the right order of magnitude for $C_p - C_v$.

Einstein torsional frequency for CH_4 can be used in a potential energy expression such as that of Gutowsky, Pake, and Bersohn to calculate the activation energy for flipping. The result is in good agreement with the low barrier reported by Tomita from nuclear magnetic resonance studies. It is suggested that Tomita's high barrier corresponds to another process in the solid, perhaps self-diffusion.

M. R. CARRIKER (Zoology): *Biology and Propagation of the Hard Clam.* (See **72:** 57–60.)

Eleven full members and sixty-two associate members were received into the Society. Otto Stuhlman and T. F. Hickerson were elected Honorary Members.

523RD MEETING, NOVEMBER 8, 1955

W. R. MANN (Mathematics): *Finite Difference Approximations to Differential Equations.* The purpose of this paper is to illustrate a method for approximating differential equations with difference equations more closely than is done with the usual finite difference approaches, but without introducing higher order differences. The method involves using a "star" having no greater thickness, in the direction of any one independent variable, than the order of the differential equation being approximated. Using such a star, further reduction in truncation error is achieved by properly adjusting the "weights" with which the various points enter. This paper is largely taken up with an illustration of the usefulness of the method in the solution of a two-region, two-dimensional, one-group reactor problem which is simple enough to be solved analytically. Numerical data, obtained on the ORACLE of the Oak Ridge National Laboratory, enable a comparison of the analytical solution for the buckling with values obtained by the ordinary difference methods and those obtained by the refined process presented in this paper. The results show that the refined process gives significantly greater accuracy than the ordinary difference methods, and the cost in increased labor is comparatively small.

T. C. BUTLER (Pharmacology): *Quantitative Studies of the Metabolic Fate of Some Drugs Used in the Treatment of Epilepsy.* The antiepileptic drugs included in this study are a series of N-methylated derivatives of barbituric acid, hydantoin, and 2,4-oxazolidinedione. It has been believed by some workers in this field that the substitution of a methyl group on nitrogen specifically enhances antiepileptic activity relative to undesirable actions. The methyl group is metabolically removed from nitrogen in compounds of this type, the reaction being nearly quantitative with all of the drugs in this series. Mephobarbital (1-methyl-5-ethyl-5-phenyl barbituric acid) is converted to phenobarbital (5-ethyl-5-phenyl barbituric acid). Metharbital (1-methyl-5,5-diethyl barbituric acid) is converted to barbital (5,5-diethyl barbituric acid). Mesantoin (3-methyl-5-ethyl-5-phenyl hydantoin) is converted to nirvanol (5-ethyl-5-phenyl hydantoin). Trimethadione (3,5,5-trimethyl-2,4-oxazolidinedione) is converted to 5,5-dimethyl-2,4-oxazolidinedione. Paramethadione (3,5-dimethyl-5-ethyl-2,4-oxazolidinedione) is converted to 5-ethyl-5-methyl-2,4-oxazolidinedione.

Ultraviolet spectrophotometric methods have been developed for the analytical determination of the demethylated products in plasma. This has permitted studies of the course of the production and elimination of the demethylated products. The demethylation reactions are slow, many hours being required for their completion. However, the elimination of the demethylated products is much slower. When a single dose of a methylated drug is given, the demethylated product persists in the body for several days after the original drug has disappeared. If repeated doses of a methylated drug are given, the demethylated product accumulates to reach a concentration much higher than that of the unchanged drug. It appears likely that these N-methylated antiepileptic drugs

actually produce the major part at least of their therapeutic effect through the demethylated products into which they are converted in the body.

Four full members and eleven associate members were elected into the Society.

524TH MEETING, DECEMBER 13, 1955

L. M. SLIFKIN (Physics): *The Physics of Semi-Conductors.*

J. J. MELLINGER (Psychology): *An Empirical Investigation of Psychological Color Space.* The isolation of attributes of experience is an old problem in psychology. In the case of color, Newton's hue circle was the pioneering work. Since that time many color classification systems have been proposed; the three-dimensional color pyramids commonly seen in psychology textbooks serve as contemporary examples. However, the color solids which have been devised so far are essentially intuitive, based upon methods such as introspection.

The problem of a metric color space, introduced by Helmholtz, is particularly intriguing. In such a space the goal is to arrange color-points so that geometric distances between points correspond to perceived differences between colors. The coordinate axes of the space, if uniquely located, would correspond to attributes of color experience. It is a question of empirical fact whether observers perceive relations between colors so that such a space can be constructed.

The experiment utilized the method of multidimensional psychophysics. The basic idea of the method is to deduce the spatial positions of a number of points, given the mutual distances between the points. If the distances between three points are 3, 4, and 5, we can infer that the points lie in two-space and in fact form a right triangle. The method of analysis is general and not confined to two or three dimensions.

With respect to colors, the problem is to obtain experimentally the psychological distances between colors and then determine analytically the dimensionality of the space and the coordinates of the color-points. Fifty subjects judged all possible pairs of 26 color chips. The 325 pairs were presented one at a time. The subject's task was to state how different the colors in each pair looked, using a nine point rating scale. The average rating for each pair was converted to a distance by using appropriate psychological scaling methods. Judgment reliability correlations of .99 and .97 were obtained.

The distances among the 26 colors were found to imply a Euclidean six-space. On comparing predicted distances with observed distances, we found the absolute discrepancy to average about 3 per cent of the observed distances. White, gray, and black were arranged along one axis, and this dimension or attribute was labeled lightness. The five other axes corresponded to five hues. Thus the standard hue circle was not verified; the five hues were found to be separate and linearly independent perceptual dimensions. In particular, purple was not seen as a combination of blue and red. Perceptual color opposites were not found. Validity correlations with Munsell calibrations were .96 (lightness) and .87 (saturation). Because of these high correlations and because of the low error

between model and data, it was concluded that a portion of psychological color space has been established.

525TH MEETING, JANUARY 10, 1956

B. G. GREENBERG (Biostatistics) AND C. M. CAMERON (Public Health Administration): *The Influence of Poliomyelitis Vaccine on Reported Poliomyelitis Incidence in North Carolina.* Review of the "Francis Report" dealing with the Salk poliomyelitis vaccine showed that the effectiveness of the vaccine in preventing all types of poliomyelitis is 49 per cent and in preventing paralytic poliomyelitis 72 per cent.

Based upon these results and the North Carolina poliomyelitis experience during the last five years, predictions were made as to how many cases of poliomyelitis the state could expect in "high," "low," and "average" incidence years. For instance, North Carolinians in 1955 will experience 630 cases of poliomyelitis if it is an average year, 409 cases if it is a low incidence year, and 987 if a high incidence year. If one-fourth of all persons in the state received vaccine, the expected number of reported cases in the average year would be reduced to about 553, and if every citizen of the state received vaccine, 321 cases of poliomyelitis should still be expected. This is a result of the inherent limitations in the vaccine as used in 1954.

While preliminary reports from state health departments for the 1955 vaccine indicate that poliomyelitis cases among children who received inoculations may have occurred at a rate lower than among other children, these figures do not actually prove that the vaccine is of value. The children who did not receive the vaccine were observed for a longer period of time than those who received one or two inoculations of vaccine during the course of the year. This means that children without vaccine had a longer period of exposure during which they could have contacted the disease, since records on inoculated youngsters date only from the time the last inoculation was given. This difference in period of exposure could account for most of the differences in poliomyelitis rates between these two groups.

C. R. BELL (Botany): *Natural Hybrids in Pitcher Plants* (Sarracenia). (See **72:** 142–152.)

526TH MEETING, FEBRUARY 14, 1956

R. L. MCKEE (Chemistry): *Some Heterocyclic Guanadines.*

J. S. MCNERNEY (Mathematics): *A Matrix Inequality and a New Integral.*

527TH MEETING, MARCH 13, 1956

JOSEPH PORTNOY (Public Health): *The* Treponema pallidum *Complement Fixation (TPCF) Test for Syphilis.* Just fifty years ago Wassermann applied the principle of complement fixation to the diagnosis of syphilis. From this beginning, identification of the antigen as lipid, refinements of the antigen, development of standardized procedures, and other improvements have been made. In spite of the apparent non-specific nature of the lipid antigens, which are derived from

mammalian tissues, serologic tests for syphilis employing these antigens have been of great value in the diagnosis, treatment, and control of syphilis.

It has been recognized, however, that these serologic tests can give rise to so-called "biologic false positive reactions" in non-syphilitic individuals. This has stimulated a search for more specific tests, involving in part the utilization of the infecting organism, *T. pallidum*.

The development of treponemal tests has been severely hampered by the inability to cultivate the organism *in vitro*. Nevertheless progress has been made. Beginning with the discovery of the *Treponema pallidum* Immobilization (TPI) Test by Nelson and Mayer, a variety of serologic procedures have been published which use treponemes isolated from infected rabbit testes as antigen.

Because of the technical limitations of the aforementioned treponemal procedures which use whole organisms, as well as the need for furthering our knowledge of the antigenic composition of *T. pallidum*, fractionation studies of these organisms were undertaken. As a result, a serologically active fraction was obtained which could be used in a conventional complement fixation test, designated as the TPCF test.

Studies accomplished point to the separate identity of reagin (antibody detected by lipid antigens), TPI, and TPCF antibodies. Results obtained suggest that the TPCF test may be as effective as the TPI test in distinguishing latent syphilis from the "biologic false positive." The simplicity of the TPCF test and the commercial availability of the antigen should make it possible for the well-run serologic laboratory to perform this test.

W. L. SMITH (Mathematical Statistics): *The Scope and Purpose of Congestion Theory.*

528TH MEETING, APRIL 10, 1956

C. E. JENNER (Zoology): *Studies on the Ecology of the Marine Snail* Narsarius obsoletus.

PETER P. VAUGHN (Anatomy): *Additional Evidence for Early Dichotomy in Reptilian Phylogeny.* The concept developed by E. S. Goodrich of an early dichotomy—into theropsid and sauropsid reptiles—in reptilian phylogeny has received its only real support until this time from the evidence of the differential division of the conus arteriosus in the two groups and from the evidence, demonstrated by D. M. S. Watson, of differential evolution of the otic notch.

Watson's idea that the theropsids altogether lacked a tympanic membrane is rejected on the basis of the presence of vestiges of the hyostapes in mammal-like reptiles and in mammalian embryos. Rather, the theories of T. S. Westoll on the homology of the amphibian tympanic membrane with the pars flaccida of the mammalian membrane seem, when combined with the basic propositions of Watson, to provide a reasonable explanation for the position of the chorda tympani dorsal to the tympanic diverticulum in living reptiles and ventral to the pars flaccida in mammals—descendants of the theropsids.

The chorda tympani of the theropsids probably lay in its primitive position posteroventral to the original (labyrinthodont) tympanic diverticulum. In the

later theropsids, a more ventral diverticulum (recessus mandibularis of Westoll) probably pushed out ventral to the chorda tympani to end laterally, in the region of the angular bone, at the developing pars tensa. This would account for the presence of the chorda tympani in the posterior malleolar fold—between the partes tensa and flaccida—of the mammalian tympanic membrane.

During the process of otic notch expansion in the evolution to sauropsids the chorda tympani was probably pulled anteriorly through a still thick tympanic "membrane" as a result of the removal of the hind end of the mandible to a more anterior position. Subsequent thinning of the membrane probably forced the nerve up against the posterior surface of the quadrate bone.

The relationships of the chorda tympani and tympanic membrane are thus seen to support Watson's thesis that the structure of the middle ear is evidence of early reptilian dichotomy and a key to the two resultant groups.

The problem of satisfactory administration of the Coker Award was discussed. It was decided to continue with the system this year, but to refer the issue to a special committee which would report next fall.

529TH MEETING, MAY 8, 1956

The Coker Award for this year was presented to Claude Piantadosi for a dissertation on organic compounds. He gave a brief outline of one phase of his work.

The Treasurer's report was read and the accounts reported in order by the Auditing Committee (G. O. Doak and J. C. Morrow).

The Nominating Committee (H. C. Crockford, Chairman, J. F. Dashiell, and J. C. Andrews) presented the following nominees for 1956–57:

President—W. L. Engels

Vice-President—E. D. Palmatier

These nominees were unanimously elected.

HAROLD G. MCCURDY, *Sec.-Treas.*

NEW SPECIES OF *SPHECODES* FROM THE EASTERN UNITED STATES[1]

BY THEODORE B. MITCHELL

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Sphecodes is a genus of parasitic bees in the family Halictidae. It is thought to be parasitic primarily upon certain of the non-parasitic genera in this same

[1] Contribution from the Entomology Department, North Carolina Agricultural Experiment Station. Published with the approval of the Director as Paper No. 740 of the Journal Series.

family, chiefly *Halictus* and *Lasioglossum*. However, specimens of at least one of the new species described in this paper have been collected in association with the andrenid genus *Calliopsis*, and there is a strong possibility that *Perdita*, another andrenid, also may be a host.

There are 35 or more species of *Sphecodes* in the United States east of the Mississippi, and at least 25 of these occur in North Carolina. This includes the 16 apparently new species described herein, 12 of which are found in North Carolina.

A key to all of these eastern species will be published in a forthcoming comprehensive work on the entire family. These new species are described at this time to make the names available to another student of the Hymenoptera who plans a revision of the genus.

Sphecodes brachycephalus sp. nov.

FEMALE.—Length 5.5 mm.; head and thorax black, abdomen ferruginous; head very much broader than long; eyes subparallel; clypeus extremely short and broad, its breadth about 4 times the length, rather flat, only slightly convex medially; labrum nearly as long as broad, rather narrowly rounded apically, dull ferruginous becoming piceous at base; mandibles slender and somewhat elongate, with a very minute and obscure inner subapical tooth, brownish-testaceous medially becoming dark at base and reddened apically; antennae black at base becoming brownish-red apically, segments 1, 2 and 3 of flagellum broader than long, the following segments about as long as broad; lateral ocelli considerably nearer to each other than to eyes; face below ocelli shining, very minutely punctate, the punctures distinctly but not widely separated, becoming slightly coarser below where they are partially obscured by the tomentum, the supraclypeal area very broad, punctures very fine and well separated, those on clypeus minute and rather close across the upper margin, becoming somewhat more deep and distinct but rather sparse and irregular apically; vertex between eyes and ocelli shining, punctures exceedingly minute and quite sparse, hind margin only very obscurely roughened, cheeks somewhat shining, with exceedingly minute and obscure but rather close punctures above, becoming smooth and shining below; wings subhyaline, with the usual 3 submarginal cells; veins pale testaceous, the stigma more brownish-piceous, tegulae testaceous-hyaline; legs brownish-piceous basally, becoming more brownish-testaceous apically; scutum and scutellum shining, punctures exceedingly minute and quite indistinct, well separated on scutum except at extreme sides and narrowly across anterior margin, those on scutellum quite sparse, minute and obscure; pleura dull, finely rugose, the hypoepimeral area shining, with a few minute and obscure punctures; dorsal area of propodeum with a basal fringe of very short striae, the apical portion smooth and shining, lateral faces dull, subrugoso-striate, the posterior face with a few obscure and shallow reticulations; abdominal terga smooth and shining, basal segment impunctate, the 2nd with minute but rather distinct and close punctures across basal half, apical half practically impunctate, the 3rd and 4th segments more fully and uniformly finely and closely punctate, apical margins of all segments rather broadly depressed and impunctate, distinctly yellowish-hyaline.

MALE.— Length 5 mm.; head and thorax black, abdomen ferruginous basally, becoming black apically; head very slightly broader than long; eyes very slightly convergent below; clypeus short and very broad, with a very slight median impression, only slightly convex; mandibles testaceous, becoming somewhat darker basally; antennae black basally, flagellum becoming somewhat more brownish-piceous apically, 1st and 2nd segments of flagellum slightly broader

than long, following segments with length and breadth subequal; lateral ocelli slightly nearer each other than to eyes; face rather thinly white pubescent, exposing the surface even below, somewhat shining, punctures minute and slightly separated between eyes and antennae, those on supraclypeal area slightly deeper and more distinct, well separated, those on clypeus equally fine and similarly spaced along basal margin, becoming slightly more coarse and close apically, face above antennae shining, punctures minute and indistinct, slightly separated, becoming even more minute on vertex between eyes and ocelli, hind margin becoming somewhat roughened and dull; cheeks above rather smooth but only very obscurely punctate, lower surface becoming smooth and shining; wings subhyaline, with the usual 3 submarginal cells, veins pale testaceous, the more basal veins and stigma more brownish-piceous; tegulae brownish-testaceous; legs piceous in large part, the more apical tarsal segments becoming brownish-testaceous; scutum and scutellum shining, punctures minute and indistinct, well separated over most of scutum becoming somewhat more close and distinct laterally and anteriorly, those on scutellum very minute and obscure; pleura dull, relatively smooth, being only subrugose anteriorly and above, but the hypoepimeral area smooth and shining, with a few very shallow and obscure punctures; dorsal area of propodeum very narrowly, finely and irregularly striate along basal margin, the apical portion rounded, smooth and shining, lateral faces dull, subrugose, and posterior face subrugose; abdominal terga smooth and shining, basal segment practically impunctate, 2nd with very fine and rather close punctures across base, these becoming very sparse apically, the 3rd somewhat more fully punctate, the apical margin of all segments rather broadly impressed, impunctate, conspicuously yellowish-hyaline; gonostyli barely reaching tips of the penis valves, very slender, with an apical slender finger-like projection which bears a few very fine setae.

HOLOTYPE: Female, Raleigh, N. C., May 19, 1950 (T. B. Mitchell, at nest site of *Calliopsis andreniformis*). Allotype, topotypical.

PARATYPES: NORTH CAROLINA: 2♂♂, 2♀♀, topotypical, 3♀♀, Wayne Co., May 7 & 23, 1954 (on *Asclepias*); 5♂♂, 4♀♀, Long Beach, May 13, 1955 (all Mitchell); 2♂♂, 2♀♀, Raleigh, May 8, 1950 (R. L. Rabb); 1♂, 1♀, Raleigh, Apr. 19, & May 8, 1950, (L. U. Chandler); 1♀, Taylors' Bridge, Sampson Co., May 24, 1954 (H. K. Townes); 1♀, New River, April & May, 1942 (G. E. Bohart). FLORIDA: 5♂♂, 5♀♀, Orlando, Apr. 4, 1955 (on sand); 3♂♂, Juniper Springs, Apr. 5, 1953; 1♂, 2♀♀, Orlando, Apr. 4, 1953; 11♂♂, 14♀♀, Orlando, Apr. 3, 1954 (on sand flat) (all K. V. Krombein); 1♀, Levy Co., May 6, 1955 (H. V. Weems, Jr.); 2♀♀, Alachua Co., Apr. 7 & 17, 1955 (Morse & Weems); 1♂, Greenville, Madison Co., Apr. 23, 1924 (T. H. Hubbell); 2♂♂, 4♀♀, Orlando, Apr. 8, 1955 (H. E. Evans); 1♂, 1♀, Welaka, May 1–4, 1955 (H. E. & M. A. Evans).

This species apparently is closely related to *antennariae* Rob., but there is insufficient material of that species at hand for comparison. The presence of three submarginal cells in *brachycephalus* might seem to be sufficient to separate it from *antennariae*, which is described as having two submarginals, but this character is a rather unstable one. A male *antennariae* which has been compared with the Robertson material has two submarginals, owing to the loss of the first transverse cubital vein. The male genital armature in this specimen is somewhat different from that of the males of *brachycephalus*. At hand also is a female identified as *antennariae* but not compared with the type. This has two submarginals, but the lost vein is the second transverse cubital rather than the first. The clypeus in this specimen is quite flat, in agreement with the description, whereas in *brachycepha-*

lus the clypeus is slightly convex. The extreme breadth of the head, with the correspondingly broad and very short clypeus, readily distinguishes *brachycephalus* from any of the other eastern species.

The evidence upon which the association of the sexes of this species is based seems quite conclusive. The sculpture of the propodeum and the form of the clypeus suggest their common identity, and the two have been found flying over a nesting area at the same time.

Sphecodes autumnalis sp. nov.

FEMALE.—Length 4 mm.; head and thorax black, abdomen brownish-testaceous, more or less suffused with piceous; head much broader than long; eyes very slightly convergent below; clypeus slightly convex; labrum broadly rounded, slightly broader than long, yellowish-testaceous; mandibles with a slight inner subapical tooth, brown-testaceous becoming reddened at tip; antennae dark basally, the flagellum more brownish-ferruginous, the more basal segments considerably broader than long, becoming nearly as long as broad apically; lateral ocelli slightly nearer to each other than to eyes; face below ocelli shining, punctures very minute but quite distinct, slightly separated but not sparse, those on lower portion of face obscured by the whitish tomentum, the supraclypeal area rather dull, very finely and rather closely punctate, punctures on clypeus fine and rather close and obscure along upper margin, becoming somewhat more distinct but still very fine and rather sparse apically; vertex between eyes and ocelli shining, punctures exceedingly minute and obscure, rather widely separated, hind margin obscurely roughened, cheeks above somewhat shining, with scattered minute and rather indistinct punctures, the lower surface smooth and shining; wings lightly infuscated, with the usual 3 submarginal cells, veins and stigma brownish-testaceous; tegulae yellowish-hyaline; legs brownish-testaceous; scutum and scutellum shining, punctures on scutum minute and rather widely separated but not sparse, somewhat more sparse on scutellum; pleura dull, finely rugose, the hypoepimeral area smooth and shining, with a few scattered exceedingly minute and obscure punctures; dorsal area of propodeum rather broad, completely but rather finely striate, lateral faces rather smooth but dull, becoming rather coarsely rugoso-striate posteriorly, and posterior face with a few irregular reticulations; abdominal terga smooth and shining, basal segment impunctate, the 2nd and 3rd with minute and rather close punctures over most of discs, becoming somewhat more sparse apically, the apical margins rather broadly impressed, yellowish-hyaline.

MALE.—Length 4–5 mm.; head and thorax black, abdomen ferruginous, becoming blackened apically; head slightly broader than long; eyes very slightly convergent below; clypeus rather broad, broadly convex; mandibles brownish-testaceous, tips becoming reddened; antennae blackish, flagellum becoming brownish-piceous beneath apically, segments 1 and 2 slightly broader than long, following segments about as long as broad; lateral ocelli subequally distant from eyes and each other; lower half of face obscured by dense white tomentum, upper portion shining, very finely but rather distinctly punctate, the punctures slightly separated, becoming minute and obscure on vertex between eyes and ocelli where the surface is shining, becoming obscurely substriate posteriorly; cheeks shining, minutely punctate, punctures rather close just back of eye, becoming more sparse posteriorly and below, lower surface smooth and shining; wings hyaline, with the usual 3 submarginal cells, veins pale testaceous, stigma more brownish-testaceous; tegulae yellowish-hyaline; legs piceous, tarsi more or less brownish-testaceous; scutum and scutellum shining, punctures very fine but

rather distinct, well separated but not sparse, and evenly distributed over most of scutum, those on scutellum somewhat more widely separated; pleura dull but quite smooth, rugose anteriorly but becoming smooth and somewhat shining posteriorly, the hypoepimeral area shining, with a few minute and obscure punctures; dorsal area of propodeum finely, irregularly, and incompletely striate, the hind margin smooth and rounded, lateral faces somewhat shining, rather smooth, becoming substriate below, posterior face with a few obscure reticulations; abdominal terga smooth and shining, basal segment with a few scattered, exceedingly minute punctures, 2nd and 3rd minutely but more distinctly and closely punctate over most of discs, apical margins of all segments rather broadly impressed, entirely impunctate, bright yellowish-hyaline; gonostyli barely attaining tips of penis valves, slender and simple, very slightly dilated apically, lower surface of gonocoxite narrowly fringed with short pubescence.

HOLOTYPE: Female, Southern Pines, N. C., Sept. 23, 1950. Allotype, topotypical, (both T. B. Mitchell).

PARATYPES: NORTH CAROLINA: 1♂, 5♀♀, topotypical; 1♀, Southern Pines, Sept. 30, 1951; 3♂♂, 11♀♀, Southern Pines, Sept. 19, 1953 (flying over sand); 1♀, Southern Pines, Sept. 19, 1953 (on *Chrysopsis*) (all Mitchell); 1♀, Southern Pines, Oct. 6, 1949 (H. & A. Howden); 1♀, The Cliffs State Park, Oct. 21, 1955 (Mitchell, on *Haplopappus*). NEW YORK: 2♂♂, 9♀♀, Ithaca, Aug. 30, 1947; 3♀♀, Ithaca, Aug. 31, 1947 (both C. Robinson); 1♀, Ithaca, Aug. 20, 1955 (K. V. Krombein); 1♀, New Russia, Essex Co., Aug. 18-31, 1912 (J. C. Bradley). MICHIGAN: 1♀, Shiawassee Co., Sept. 3, 1950; 2♀♀, Midland Co., Aug. 28, 1948; 1♀, Gladwin Co., Aug. 28, 1948 (all R. R. Dreisbach). ONTARIO, CANADA: 3♀♀, Ottawa, Aug. 31, 1947 (W. R. M. Mason).

Autumnalis could be confused with *brachycephalus*, but in the female the head is less broad, and the clypeus is more rounded. In both sexes the dorsal face of the propodeum is more completely striate, however, with the posterior margin smooth and somewhat rounded. These two species differ in their seasonal flight, *autumnalis* occurring in August and September in the northern states, September and October in North Carolina, whereas *brachycephalus* is vernal, flying in April and May. The range evidently differs also, the type series of *autumnalis* including specimens from North Carolina, New York, Michigan and Ontario, while *brachycephalus* is recorded so far only from North Carolina and Florida.

The evidence for the association of the sexes of this species seems reasonably conclusive. The sculpture of the pleura and propodeum is quite similar in both and the form of the clypeus is much the same. Moreover, the two sexes have been collected in flight together both at Southern Pines, N. C. and at Ithaca, N. Y.

Sphecodes wheeleri sp. nov.

FEMALE.—Length 6 mm.; head and thorax black, abdomen ferruginous, becoming piceous apically; head much broader than long; eyes slightly convergent below; clypeus broad and rather short, slightly convex; labrum broadly rounded, dark reddish-ferruginous apically, more or less blackened basally; mandibles entirely simple, brownish-testaceous, more or less piceous at tips; antennae blackened basally, the flagella brownish-ferruginous, basal segment shorter than broad, subequal to pedicel, the second similar to the first, 3rd and following segments about as broad as long; lateral ocelli very slightly nearer to each other than to eyes; face below ocelli somewhat shining, punctures deep and distinct,

quite close but not crowded, becoming very fine and rather obscure below, those on the supraclypeal area quite close, deep and rather coarse, those on clypeus more widely separated but deep and distinct; vertex between eyes and ocelli shining, becoming obscurely and finely striate along hind margin and on cheeks below; wings subhyaline, with but two submarginal cells, veins and stigma brownish-piceous; tegulae testaceous-hyaline; legs brownish-ferruginous basally, the tibiae more or less testaceous medially and the tarsi becoming testaceous apically; scutum and scutellum rather dull, punctures deep and distinct, well separated over posterior half of scutum but becoming very close and obscure, more rugoso-punctate, anteriorly, the scutellum slightly grooved medially, punctures more obscure but well separated, becoming quite close laterally; pleura coarsely reticulate; dorsal area of propodeum coarsely, completely and regularly striate, lateral faces rather finely and irregularly striate, posterior face very coarsely reticulate; abdominal terga shining, basal segment practically impunctate, the 2nd and 3rd with exceedingly minute punctures, these rather close laterally, somewhat more widely separated but more minute and indistinct medially, apical margins of all segments very broadly yellowish-hyaline and impunctate.

MALE.—Length 5–6 mm.; head and thorax black, and abdomen largely or entirely black; head considerably broader than long; eyes rather strongly convergent below; clypeus only slightly convex; mandibles brownish-testaceous, with tip slightly reddened, base more or less piceous; antennae dark basally, flagellum more or less brownish-piceous, segments barely as long as they are broad, basal segment slightly shorter; lateral ocelli very slightly nearer to each other than to eyes; lower portion of face laterally obscured by dense pale tomentum, but clypeus and supraclypeal area partially exposed, punctures fine and rather close, those on supraclypeal area somewhat coarser than on clypeus, upper portion of face rather dull, punctures quite deep and distinct, rather fine and very close, becoming rather sparse on the shining vertex between eyes and ocelli, hind margin becoming obscurely transversely striate, cheeks somewhat shining above, becoming finely striate posteriorly and below, but lower surface relatively smooth; wings subhyaline, with but two submarginal cells, veins yellowish-testaceous, stigma somewhat more brownish-testaceous; tegulae yellowish-hyaline; legs piceous basally, tarsi somewhat more yellowish; scutum rather dull, anterior half obscurely and shallowly rugoso-punctate, becoming somewhat smoother posteriorly, where the punctures are distinct but rather fine, quite sparse except along hind border, those on scutellum rather fine and shallow, quite sparse except at extreme sides; pleura coarsely reticulate; dorsal area of propodeum completely and quite coarsely and regularly striate, lateral faces finely striate anteriorly becoming coarsely reticulate posteriorly, and posterior face coarsely reticulate; abdominal terga smooth and shining, basal segment with scattered, exceedingly minute sparse punctures, 2nd and 3rd segments very finely and rather closely punctate over most of disc, becoming slightly more sparse toward the rather broad, entirely impunctate, impressed apical margin which is more or less testaceous along rim; gonostyli rather short, compressed on each side of a median carina, the inner side angulate medially, outer side broadly spatulate apically, only slightly exceeding penis valves; gonocoxites densely tomentose on lower surface.

HOLOTYPE: Female, Marion, N. C., June 18, 1941 (T. B. Mitchell, on *Leucanthemum*).

ALLOTYPE: Smokemont, N. C., July 20, 1923 (Mitchell). PARATYPES: NORTH CAROLINA: 1♀, Raleigh, N. C., May 4, 1952 (H. & A. Howden); 1♂, Judson, July 19, 1923 (Mitchell, on

Hydrangea). NEW YORK: 2♂♂, Ithaca, Aug. 2 & 30, 1947 (C. Robinson). CONNECTICUT: 1♀, Colebrook, Aug. 13, 1922; 3♂♂, Colebrook, July 24, 1921; 1♂, Colebrook, Aug. 6, 1922; 1♂, Colebrook, Aug. 27, 1919; 1♂, Colebrook, Sept. 6, 1919 (all W. M. Wheeler) [M. C. Z.].

This species is very similar to *pimpinellae* Rob., but lacks the distinct inner subapical mandibular tooth of that species. Other differences, such as the slightly shorter labrum and the darker color of the labrum, basal segments of the legs and the wing veins and stigma, may or may not be constant. There are no males of *pimpinellae* at hand for comparison, and the matter of its identity and the correctness of the association of the two sexes of *wheeleri* needs further study.

All of these specimens are similar in lacking the first transverse cubital vein in the front wing, thus having but two submarginal cells, and this character may be constant in this species.

Sphecodes townesi sp. nov.

FEMALE.—Length 6 mm.; head and thorax black, abdomen ferruginous becoming darkened apically; head much broader than long; eyes slightly convergent below; clypeus rather evenly convex; labrum quite short, broadly rounded, dark; mandibles with a distinct inner subapical tooth, dark basally, becoming ferruginous apically; antennae dark basally, becoming more brownish-piceous apically, basal segment of flagellum slightly broader than long, the 2nd about as long as broad and the following segments slightly longer than broad; lateral ocelli slightly nearer to each other than to eyes; face below ocelli dull, punctures rather fine but deep and distinct, closely crowded, becoming somewhat more distinctly separated below, but obscured by the pubescence, those on supraclypeal area fine and rather close but distinctly separated, those on clypeus somewhat coarser, rather close across upper margin but becoming rather sparse and irregular apically; vertex between eyes and ocelli somewhat shining, punctures fine, distinct and slightly separated, hind margin becoming obscurely rugose, cheeks somewhat shining above, with very vague and indistinct but rather close punctures, becoming quite smooth below; wings lightly infuscated, with the usual 3 submarginal cells, veins and stigma brownish-piceous; tegulae testaceous-hyaline; legs piceous; scutum and scutellum somewhat shining, punctures rather coarse, quite deep and distinct, slightly separated over scutum medially, becoming finally rugoso-punctate along the anterior margin narrowly, and quite close across posterior margin, scutellum very slightly impressed medially, punctures irregularly scattered and rather sparse; pleura coarsely rugose but the hypoepimeral area shining, with a few scattered shallow and rather obscure punctures; dorsal area of propodeum completely and rather coarsely striate, lateral faces dull, finely rugoso-striate, the posterior face reticulate; abdominal terga smooth and shining, basal segment practically impunctate, 2nd and 3rd with very minute and rather close punctures across basal half, apical half becoming practically impunctate, apical margins rather broadly impressed, only the 2nd obscurely yellowish-hyaline.

HOLOTYPE: Female, Sunburst, N. C., June 26, 1934 (T. B. Mitchell).

PARATYPES: NORTH CAROLINA: 1♀, Busick—Mt. Mitchell Trail, June 20, 1941 (Mitchell). MICHIGAN: 1♀, Iosco Co., May 30, 1951 (R. R. Dreisbach). NEW YORK: 3♀♀, Ithaca, June 11, 1935 (H. K. Townes).

The punctures of the face below the ocelli are so closely crowded as to be nearly

indistinguishable. This feature, in conjunction with the smooth and shining hypoepimeral area of the pleura, will about serve as a means of recognition.

Sphecodes morsei sp. nov.

FEMALE.—Length 5 mm.; head and thorax shining black, abdomen ferruginous basally, the apical half blackened; head much broader than long; eyes slightly convergent below; clypeus broadly convex; labrum rather short and broad, broadly rounded, dull reddish apically, becoming somewhat darker at base; mandibles with a distinct and rather robust inner subapical tooth, testaceous medially becoming piceous at base and reddened at tip; antennae blackish basally, the flagellum dull brownish-ferruginous beneath, more piceous above, the more basal segments of the flagellum somewhat broader than long, these becoming longer apically where the length slightly exceeds the breadth; lateral ocelli slightly nearer to each other than to eyes; face below ocelli shining, punctures very fine but deep and distinct and widely separated, almost sparse, becoming relatively close but more shallow and obscure below, the supraclypeal area slightly elevated, punctures very fine, irregular, slightly separated, those on clypeus fine and rather close along upper margin, becoming somewhat more coarse, deep and much more sparse apically; vertex between eyes and ocelli polished, punctures minute and sparse, hind margin becoming rather coarsely transversely striate, cheeks above rather dull, finely striate, becoming rather smooth and shining below; wings subhyaline, with the usual 3 submarginal cells, veins and stigma brownish-testaceous; tegulae brownish-testaceous; legs piceous basally, becoming more brownish-testaceous on tarsi; scutum and scutellum polished, punctures deep and distinct but very fine and widely separated even between notaulices and tegulae, those on scutellum also very sparse; pleura dull, quite densely rugose; dorsal area of propodeum quite broad, completely and rather coarsely rugoso-striate, lateral and posterior faces rather coarsely reticulate; abdominal terga smooth and shining, basal segment entirely impunctate, the 2nd and 3rd with a few, scattered, rather sparse, exceedingly minute and obscure punctures toward the base, apical margins of all segments rather broadly impressed, impunctate, those of the 1st and 2nd segments yellowish-hyaline, the others only very narrowly so along the rims.

HOLOTYPE: Female, Ascutney, Vt., Aug. 14 (A. P. Morse) [M. C. Z.].

PARATYPE: 1 ♀, Cramer, Minn., Aug. 10, 1922 (H. H. Knight) [Univ. Minn.].

The polished surface of the face between the ocelli and antennae, with the fine, widely separated punctures, sets this species apart from any of the other eastern species.

Sphecodes australis sp. nov.

MALE.—Length 6 mm.; head and thorax black, abdomen entirely black, or ferruginous basally, becoming black apically; head considerably broader than long; eyes very slightly convergent below; clypeus broadly convex; mandibles entirely dark; antennae black basally, flagellum somewhat more piceous, basal segment slightly broader than long, the 2nd and following segments nearly twice this length, entirely simple; lateral ocelli subequally distant from eyes and each other; face only thinly pubescent, the surface fully exposed, punctures rather coarse and close in general, being somewhat finer between antennae and eyes and along apical margin of supraclypeal area, those on clypeus quite coarse,

deep, and close throughout, area above antennae dull, coarsely and deeply punctate, the punctures crowded, becoming more distinctly separated on vertex between eyes and ocelli, hind margin becoming coarsely reticulate; cheeks above reticulate, becoming more striate below, even the lower surface being dull and substriate; wings lightly infuscated, with the usual 3 submarginal cells, veins and stigma brownish-testaceous; tegulae brownish-testaceous, becoming yellowish-hyaline anteriorly; legs black basally, becoming somewhat more brownish on apical tarsal segments; scutum and scutellum shining between deep and distinct punctures, these well separated over most of scutum, becoming somewhat finer and closer between notaulices and tegulae, and crowded along narrow anterior margin, scutellum very slightly impressed medially, punctures quite sparse on each side of this; pleura coarsely reticulate; dorsal area of propodeum coarsely reticulate medially, becoming more regularly striate at extreme sides, lateral faces rather finely and irregularly striate, becoming coarsely reticulate posteriorly, and posterior face coarsely reticulate; abdominal terga smooth and shining, punctures quite coarse, deep, and distinct, irregularly scattered over disc of basal segment, somewhat closer and more regular on 2nd and 3rd, distinctly but not widely separated, apical margins rather narrowly impressed, entirely impunctate, concolorous with remainder of discs; gonocoxites slightly excavated on dorsal surface basally, gonostyli considerably exceeding tips of penis valves, rather robust, strongly compressed, with a very slender terminal setose projection and a broad, membranous inner lobe.

HOLOTYPE: Male, Mt. Mitchell, N. C., 6,000 ft., June 26, 1952 (T. B. Mitchell).

PARATYPES: NORTH CAROLINA: 1♂, Raleigh, June 24, 1945 (Mitchell, on *Daucus carota*); 1♂, Sunburst, June 26, 1934 (Mitchell). VIRGINIA: 2♂♂, Falls Church, June 18, (N. Banks, on *Ceanothus*); 2♂♂, Glencarlyn, June 7, (Banks, on *Aruncus*) [M. C. Z.]. MICHIGAN: 2♂♂, Oswego Co., July 30, 1944; 1♂, Shiawassee Co., July 16, 1950 (both R. R. Dreisbach). CONNECTICUT: 3♂♂, Colebrook, Aug. 23, 1919 and July 14, 1921 (W. M. Wheeler) [M. C. Z.]. NEW YORK: 1♂, Canajoharie, Aug. 13, 1934; 1♂, Oneonta, June 30, 1935 (both H. K. Townes).

This may be the male of *S. obscurans* Lov. & Ckll.

Sphecodes hydrangeae sp. nov.

MALE.—Length 6 mm.; entirely black; head considerably broader than long; eyes very slightly convergent below; clypeus rather broadly convex; mandibles black basally, becoming reddish apically; antennae black, scape very short, basal segment of flagellum about as broad as long, second nearly twice this length, remainder of flagellum rather strongly moniliform, the more apical segments with basal, densely pilose, very short semicircular facets beneath; lateral ocelli subequally distant from eyes and each other; lower portion of face obscured by the dense white pubescence, surface of clypeus partially exposed, punctures rather fine and very close throughout, area above antennae dull, punctures deep and distinct but rather coarse and very close, becoming somewhat more distinctly separated on vertex between eyes and ocelli, hind margin becoming more reticulate, cheeks finely rugoso-punctate above, becoming rather distinctly and coarsely striate below, only a very restricted portion of ventral surface being smooth and shining; wings subhyaline, with the usual three submarginal cells, veins and stigma brownish-testaceous; tegulae yellowish-hyaline; legs blackish, only the apical tarsal segments becoming brownish; scutum and scutellum somewhat shining between the coarse and deep punctures, these well separated in center of scutum but not sparse, becoming rugoso-punctate along anterior margin, scutellum well covered with irregular deep and close punctures; pleura coarsely reticulate; dorsal area of propodeum coarsely reticulate medially,

becoming more regularly striate laterally, lateral faces striate anteriorly, becoming reticulate posteriorly, and posterior face coarsely reticulate; abdominal terga shining between the rather coarse, deep, and distinct punctures, these quite close over discs of each segment, only the rather narrow, apical, impressed area impunctate, these very slightly reddened along rim; gonocoxites rather strongly excavated on dorsal surface, the gonostyli robust, compressed, inner surface somewhat excavated, with a slender apical projection which is well covered with setae, and with a broad, submembranous inner lobe, considerably exceeding apex of penis valves.

HOLOTYPE: Male, Crusco, N. C., June 25, 1934 (T. B. Mitchell, on *Hydrangea*).

PARATYPES: 2♂♂, Colebrook, Conn., Aug. 23 & Sept. 5, 1919 (W. M. Wheeler) [M. C. Z.].

This is closely related to *confertus*, but the basal segment of the flagellum is much longer in that species, being considerably longer than broad, and the basal abdominal tergum is nearly impunctate. In contrast, the basal flagellar segment in *hydrangeae* is no longer than broad, and the basal abdominal tergum is covered with deep and distinct punctures. It is similar, also, to the male of *prosphorus*, differing chiefly in the character of the antennae, the basal pilose facets being very restricted, whereas they are very extensive in *prosphorus*, and the segments in *hydrangeae* are strongly moniliform, in contrast with those of *prosphorus*.

Sphecodes coronus sp. nov.

MALE.—Length 5 mm.; entirely black; head somewhat broader than long; eyes slightly convergent below; clypeus only slightly convex; mandibles brownish-ferruginous, tips more reddish, and becoming dark basally; antennae black basally, flagella brownish, basal segment considerably broader than long, subequal in length to pedicel, 2nd and following segments about as long as broad, the more apical ones becoming very slightly longer; lateral ocelli subequally distant from eyes and each other; lower portion of face obscured by dense white pubescence, punctures very fine and close beneath the pubescence on both sides of face, and more coarse and deep but closely crowded on clypeus, becoming somewhat finer apically; upper portion of face rather dull, punctures rather fine, deep, and distinct but closely crowded, becoming more distinctly separated on shining vertex between eyes and ocelli, hind margin becoming obscurely substriate; cheeks rather dull, very finely and obscurely striate posteriorly and below, lower surface rather smooth, somewhat shining; wings lightly infuscated, with the usual 3 submarginal cells, veins testaceous, stigma more brownish-piceous; tegulae yellowish-hyaline with dark blotches; legs piceous, only the more apical segments becoming brownish-testaceous; scutum and scutellum shining between rather coarse, deep, and distinct punctures, these well separated over most of scutum, becoming closely crowded along narrow anterior margin, somewhat finer but well separated between notaulices and tegulae, punctures of scutellum rather sparse, irregularly scattered; pleura densely rugose; dorsal area of propodeum rather broad, completely and rather closely and coarsely striate, median striae somewhat irregular, lateral faces rather finely striate anteriorly and above, becoming more coarsely reticulate or substriate posteriorly and below, posterior face coarsely reticulate; abdominal terga smooth and shining, basal segment with only a few exceedingly minute and obscure punctures scattered toward the sides, 2nd and 3rd segments finely and quite closely punctate basally, becoming sparse apically especially on 2nd tergum,

apical impressed areas entirely impunctate; gonostyli very slightly exceeding tips of the penis valves, short, somewhat constricted at base, with a very short, subtriangular, median projection above, and with a ventral, hatchet-shaped, inner lobe.

HOLOTYPE: Male, Wake County, N. C., June 16, 1955 (T. B. Mitchell, on *Daucus carota*).

PARATYPES: NORTH CAROLINA: 2♂♂, topotypical (on *D. carota* and *Rhus glabra*); 1♂, Raleigh, Aug. 19, 1930 (on *Solidago*); 1♂, Yadkin Co., June 23, 1948 (on *Rhus*); 1♂, Grandfather Mt., June 27, 1952 (on *Hydrangea*) (all Mitchell); 1♂, Pineola, Aug. 3, 1937 (D. L. Wray) [N. C. Dept. Agr.]. VIRGINIA: 1♂, Falls Church, July 16; 1♂, Glencarlyn, July 16, (on *Ceanothus*) (both N. Banks) [M. C. Z.]. NEW JERSEY: 1♂, Riverton, Aug. 13, 1924 (J. B. Cronin); 1♂, Stafford's Forge, Ocean Co., July 10, 1955 (A. F. Shinn). MICHIGAN: 1♂, Arenac Co., July 19, 1952; 1♂, Charlevoix Co., Aug. 12, 1939; 1♂, Dickinsen Co., Aug. 12, 1953; 2♂♂, Alger Co., Aug. 14, 1953 (all R. R. Dreisbach). NEW YORK: 1♂, Campus, Ithaca, July 5, 1937 (P. P. Babiy) [Cornell Univ.]; 2♂♂, Mille Lace, Minn., Oct. 9 & 21, 1938 (Mickel and Rodeck). MINNESOTA: 1♂, Anoka Co., Fridley Sand dunes, July 21, 1922 (C. E. Mickel) [Univ. Minn.]; 1♂, Westerly, R. I., Aug. 1, 1936 (M. Chapman). MASSACHUSETTS: 2♂♂, Forest Hills, Aug. 29–30, 1922 (W. M. Wheeler) [M. C. Z.]; 1♂, Needham, June 18, 1951 (Mitchell).

This may prove to be the male of one of several species in which only the female is known at this time. The type specimen is about average in size, the paratype specimens ranging from 4 mm. to nearly 6 mm. in length.

Sphecodes packardi sp. nov.

MALE.—Length 6 mm.; head and thorax black, basal segment of abdomen piceous in large part, becoming ferruginous along apical margin, the second and third terga ferruginous in part, apical terga black; head much broader than long; eyes slightly convergent below; clypeus broadly convex; mandibles dark basally, becoming brownish-testaceous apically, but the tip reddened; antennae black basally, flagellum brownish beneath, becoming somewhat more piceous above, basal segment about as broad as long, 2nd and following segments nearly twice this length, entirely simple; lateral ocelli subequally distant from eyes and each other; lower half of face including clypeus obscured by dense white pubescence, the upper portion above antennae quite coarsely and deeply punctate, the punctures crowded medially, becoming somewhat more distinct laterally, those on vertex between eyes and ocelli very fine and rather obscure, well separated, hind margin becoming irregularly transversely striate; cheeks striate, with ventral surface somewhat smoother but rather dull; wings subhyaline, with the usual 3 submarginal cells, veins and stigma testaceous; tegulae yellowish-hyaline; legs piceous basally, the front tibia and all the tarsi yellowish-testaceous; scutum and scutellum somewhat shining between rather coarse and deep punctures, these rather widely separated over most of scutum, even between notaulices and tegulae, becoming close or more rugose along anterior margin, those on scutellum quite sparse; pleura coarsely rugose; dorsal area of propodeum quite broad, rather finely reticulate medially, becoming more regularly striate laterally, lateral faces very finely and irregularly striate anteriorly, becoming coarsely reticulate posteriorly, posterior face coarsely reticulate; abdominal terga polished, punctures exceedingly minute, basal segment practically impunctate, 2nd and 3rd with a few minute and obscure sparse punctures across base, apical half practically impunctate, apical impressed areas rather broad, concolorous with remainder of discs; gonocoxites rather strongly exca-

vated dorsally toward base, gonostyli slightly exceeding tips of penis valves, rather strongly compressed, with a very short and inconspicuous, finger-like, apical projection which bears a few, short, inconspicuous setae, and with an inner, rather small, membranous lobe.

HOLOTYPE: Male, Glen House, N. H., July 24, 1915 [M. C. Z.].

PARATYPES: NEW HAMPSHIRE: 1♂, White Mts. (A. S. Packard). VERMONT: 1♂, Ascutney (A. P. Morse) [both M. C. Z.]. MINNESOTA: 1♂, Lake Co., Aug. 22, 1938 (H. E. Milliron) [Univ. Minn.].

Sphecodes exaltus sp. nov.

FEMALE.—Length 6 mm.; head and thorax black, abdomen ferruginous becoming darkened apically; head slightly broader than long; eyes very slightly convergent below; clypeus rather short, slightly convex; mandibles simple, rather elongate, brownish-testaceous with slightly reddened tip; antennae largely piceous, 1st and 2nd segments much broader than long, length and breadth of the following segments subequal; lateral ocelli slightly nearer each other than to eyes; face below ocelli shining, finely and distinctly punctate, the punctures well separated but hardly sparse, interspaces exceeding diameter of punctures over most of area, the supraclypeal area somewhat shining, with very fine and rather close shallow punctures, those on clypeus fine, shallow and rather sparse medially, becoming somewhat closer but still well separated laterally; vertex shining between eyes and ocelli, the punctures fine, distinct and well separated, hind margin becoming obscurely roughened; cheeks dull, finely and obscurely punctate above, becoming smooth and shining below; wings faintly infuscated, with the usual 3 submarginal cells, veins and stigma brownish-testaceous; tegulae testaceous-hyaline; legs piceous in general, becoming somewhat paler on apical tarsal segments; scutum and scutellum somewhat shining, punctures deep and distinct, rather fine, close over most of scutum, becoming almost crowded anteriorly, interspaces about equalling diameter of punctures in general, those on scutellum somewhat finer and more widely separated; pleura rather coarsely rugose, the hypoepimeral area rather smooth; dorsal area of propodeum coarsely and completely reticulate, lateral faces quite smooth and shining anteriorly, becoming coarsely reticulate posteriorly, the posterior face coarsely reticulate; abdominal terga smooth and shining, basal tergum impunctate, punctures of 2nd and 3rd segments quite close, evenly distributed over most of disc, apical margin of all the segments rather broadly impressed and impunctate, those on the first 3 segments yellowish-hyaline, piceous on the 4th.

HOLOTYPE: Female, Southern Pines, N. C., Sept. 23, 1950 (T. B. Mitchell).

Sphecodes crawfordi sp. nov.

FEMALE.—Length 6 mm.; head and thorax black, abdomen ferruginous basally, becoming black apically; head somewhat broader than long; eyes very slightly convergent below; clypeus short and very broad, only very slightly convex; labrum nearly as long as broad, rounded apically, entire, dark basally, becoming more ferruginous apically; mandibles simple, rather elongate, brownish-testaceous with reddened tip; antennae largely piceous, the flagellum somewhat paler brownish beneath, 1st and 2nd segments much broader than long, length and breadth of the following segments subequal; lateral ocelli slightly nearer each other than to eyes; face below ocelli finely, deeply and distinctly punctate, the punctures almost crowded just below ocelli, but becoming somewhat more widely and distinctly separated between this area and antennae, the supraclypeal area somewhat shining, with very fine and rather close shallow punctures, punctures on clypeus close along upper margin, becoming much more

coarse and sparse toward apical margin; vertex somewhat shining between eyes and ocelli, the punctures deep and distinct, quite close but not crowded, hind margin becoming finely rugoso-striate, cheeks dull, finely rugoso-striate above, becoming smooth and shining below; wings faintly infuscated, with the usual 3 submarginal cells, veins and stigma brownish-testaceous; first recurrent vein nearly contiguous with second intercubital; tegulae testaceous-hyaline; legs reddish-piceous in general, becoming somewhat paler on apical tarsal segments; scutum and scutellum somewhat shining, punctures deep and distinct, rather fine, close over most of scutum, becoming almost crowded anteriorly, interspaces not exceeding diameter of punctures in general, those on scutellum somewhat more irregular and more widely separated; pleura coarsely rugose, becoming somewhat more striate posteriorly; dorsal area of propodeum rather coarsely, completely rugoso-striate, lateral faces finely reticulate above, becoming more coarsely striate below, the posterior face coarsely reticulate; abdominal terga smooth and shining, punctures fine but quite deep and distinct, irregularly scattered and rather sparse across central portion of basal segment, those on 2nd and 3rd segments quite close, evenly distributed over most of disc, apical margin of all the segments rather broadly impressed and impunctate, those on the first two segments yellowish-hyaline, black on the 3rd and 4th.

HOLOTYPE: Female, Bryson City, N. C., Aug. 29, 1923 (J. C. Crawford) [N. C. Dept. Agr.].

Sphecodes canadensis sp. nov.

MALE.—Length 4.5–5.5 mm.; largely black, abdomen more or less suffused with ferruginous; head slightly broader than long; eyes rather strongly convergent below; clypeus strongly convex; mandibles testaceous, with a contrasting piceous tip; antennae black basally, flagellum brownish-piceous, basal segment broader than long, 2nd with length and breadth subequal, following segments very slightly longer than broad, entirely simple; lateral ocelli subequally distant from eyes and each other; lower portion of face obscured by the rather dense white pubescence, clypeus partially exposed, with rather coarse, deep, and close punctures, upper portion of face dull, punctures deep, distinct, rather fine and very close, becoming rather sparse on vertex between eyes and ocelli, hind margin somewhat shining and obscurely punctate; cheeks above rather dull, very finely and obscurely substriate, striae becoming more distinct posteriorly and below, lower surface smooth and somewhat shining; wings subhyaline, with the usual 3 submarginal cells, veins testaceous, stigma somewhat more brownish; tegulae yellowish-hyaline; legs brownish-piceous, apical tarsal segments somewhat more brownish-testaceous; scutum and scutellum shining between deep, distinct, rather coarse, and uniformly sparse punctures, these being rather widely separated even between notaulices and tegulae, becoming rather close along narrow anterior margin, those on scutellum fine and very sparse; pleura densely rugose; dorsal area of propodeum completely and rather coarsely striate, median striae more or less irregular, lateral faces dull, substriate anteriorly, becoming coarsely reticulate posteriorly, and posterior face coarsely reticulate; abdominal terga smooth and shining, basal segment nearly impunctate, 2nd and 3rd with very fine and rather close punctures across base, these becoming sparse apically, apical margins rather broadly impressed, entirely impunctate, more or less yellowish-hyaline except on the more apical segments where they are concolorous with the discs; gonocoxites abruptly truncate apically, the gonostyli slightly exceeding tips of penis valves, acute apically, but with a ventral, subapical, subtriangular lobe directed toward the mid line, practically bare.

HOLOTYPE: Male, Robeval, Que., Aug., 1910.

PARATYPES: 1♂, topotypical, [Univ. R. I.]. NORTH CAROLINA: 1♂, Forney Creek, Smoky

Mt. Nat. Park, N. C., Aug. 3–5, 1931 (Bradley and Knorr) [Cornell]. QUEBEC, CANADA: 1♂ Ellis Bay, Anticosti Isl. [M. C. Z.].

Sphecodes carolinus sp. nov.

FEMALE.—Length 6 mm.; head, thorax and apex of abdomen black, segments 1–3 of abdomen ferruginous; head distinctly broader than long, eyes very slightly convergent below; clypeus quite broad and short, slightly convex; labrum slightly broader than long, slightly rounded or subtruncate apically, smooth and shining, entirely black; mandibles dark basally, becoming ferruginous toward apex, with a distinct subapical inner tooth; antennae black basally and above, the flagellum more piceous beneath apically, basal segment of flagellum slightly broader than long, subequal to pedicel, the 2nd segment very slightly longer, the more apical segments slightly longer than broad; lateral ocelli slightly nearer each other than to eyes; face below ocelli rather dull, the punctures fine but deep, distinct and very close, almost crowded, becoming slightly more separate below, those on supraclypeal area quite deep, distinct and close, those on clypeus slightly more sparse; vertex shining between eyes and ocelli, the punctures somewhat more sparse, posterior margin back of ocelli obscurely roughened; cheeks rather dull, substriate posteriorly, becoming somewhat smoother and obscurely punctate toward outer margins of eyes, the lower surface smooth and shining; wings subhyaline, with the usual 3 submarginal cells, veins piceous to brownish, stigma more piceous; tegulae brownish-piceous; legs black in general, the more apical tarsal segments somewhat paler; scutum and scutellum shining, somewhat metallic, punctures deep and distinct, rather coarse but rather widely separated in general, even between notaulices and tegulae, disc of scutum with a shallow indistinct median groove anteriorly; pleura very coarsely rugose below, more finely rugose on hypoepimeral area; dorsal area of propodeum coarsely and completely striate, the lateral faces irregularly striate, posterior face more reticulate; abdominal terga smooth and shining, basal segment with no evident punctures, 2nd and 3rd with exceedingly minute and very sparse punctures scattered across the base, otherwise practically impunctate, the impressed apical margins broad and entirely impunctate.

HOLOTYPE: Female, Grandfather Mt., N. C., June 24, 1954 (T. B. Mitchell, on *Rubus*).

PARATYPES: NORTH CAROLINA: 2♀♀, Grandfather Mt., July 3, 1945; 1♀, Wilkesboro, June 6, 1952; 1♀, Smokemont, June 30, 1934 (on *Chrysanthemum leucanthemum*); 1♀, Raleigh, May 15, 1945 (on *Ceanothus*); 2♀♀, Raleigh, mid May, 1921 (on *C. leucanthemum*), (all Mitchell); 1♀, Raleigh, May 6, 1925 (C. S. Brimley) [N. C. Dept. Agr.]; 2♀♀, Haywood Co., June 17, 1955 (H. V. Weems, Jr., on *Acer spicatum* & *Aruncus aruncus*). TENNESSEE: 1♀, Smoky Mt. Nat. Park, (3000 ft.), June 25, 1947 (Mitchell, on *Hydrangea*). MICHIGAN: 1♀, Muskegon Co., June 30, 1951; 1♀, Iosco Co., July 23, 1950 (both R. R. Dreisbach). VIRGINIA: 2♀♀, Falls Church, May 3 & June 20, 1♀, Glencarlyn, June 17, (both N. Banks). CONNECTICUT: 1♀, Colebrook, July 5, 1921 (W. M. Wheeler); 1♀, Cambridge (Putnum). MAINE: 1♀, Mt. Katahdin, 1–3,000 ft., July 1, 1901 [all M. C. Z.]. RHODE ISLAND: 1♀, Kingston, May 14, 1951 [Univ. R. I.]. NEW JERSEY: 1♀, Pitman, June 9, 1918 [Cornell Univ.]. D. C.: 2♀♀, May 7, 1944 and July–Aug., 1944 (G. E. & R. M. Bohart). MINNESOTA: 1♀, Houston Co., May 22, 1937 (R. H. Daggy); 1♀ St. Anthony Park, June 22, 1921 (W. E. Hoffmann) [both Univ. Minn.].

This species is close to *mandibularis* Cresson, the chief differences being the larger size (6 mm.), broader face with eyes nearly parallel, and the coarsely reticulate pleura. The average size of *mandibularis* is about 5 mm., the eyes are quite distinctly convergent below, with the lower part of the face narrowed, and the pleura are rugose or finely reticulate.

Sphecodes nigricorpus sp. nov.

MALE.—Length 6 mm.; entirely black; head slightly broader than long; eyes slightly convergent below; clypeus rather strongly convex, quite broad; mandibles dark basally, reddened toward tip; antennae more brownish-piceous, basal segment of flagellum about equal to pedicel in length, 2nd segment slightly longer and succeeding segments becoming successively longer, the more apical ones somewhat longer than broad; lateral ocelli subequally distant from eyes and each other; face including clypeus quite coarsely, deeply and uniformly punctate, the punctures more distinctly separated on clypeus, almost contiguous above antennae, becoming very sparse and fine between eyes and ocelli; vertex back of ocelli obscurely substriate, the cheeks more coarsely striate behind, becoming relatively smooth and very finely punctate along outer margins of eyes, lower surface somewhat shining but finely striate; pubescence of head very thin, short, entirely white; wings subhyaline with the usual 3 submarginal cells, veins brownish-testaceous, stigma somewhat darker; tegulae piceous; legs black basally, becoming more testaceous on the apical tarsal segments; scutum and scutellum smooth and shining, the punctures very fine, widely separated on scutum posteriorly and on scutellum, becoming somewhat closer but still quite sparse on scutum anteriorly; pleura rather coarsely rugoso-reticulate; dorsal area of propodeum coarsely and quite regularly striate, lateral faces more finely reticulate, becoming somewhat more coarsely so below, posterior face coarsely reticulate; abdominal terga smooth and shining, punctures of basal segment hardly visible, 2nd and 3rd with very fine, well separated punctures toward base, becoming practically impunctate over apical half, the broad, faintly impressed apical margins entirely impunctate and very slightly reddened; gonostyli slightly exceeding penis valves, with a rather short, apical, triangular, inner expansion.

HOLOTYPE: Male, Colebrook, Conn., Aug. 3, 1922 (W. M. Wheeler) [M. C. Z.].

Sphecodes fattigi sp. nov.

MALE.—Length 6.5 mm.; head and thorax black, segments 1 and 2 of abdomen ferruginous, the 3rd suffused with piceous, the 4th and 5th piceous; head considerably broader than long, eyes convergent below; mandibles dull testaceous, somewhat reddened at tip; antennae dark reddish-piceous, basal segment of flagellum about equal to pedicel in length, 2nd and following segments slightly longer, length and breadth of each about equal; lateral ocelli subequally distant from eyes and each other; entire face including clypeus rather coarsely rugoso-punctate and dull, vertex back of ocelli becoming more coarsely reticulate, the cheeks coarsely reticulate with only a narrow area beneath becoming smooth and shining; facial pubescence white and rather short, thin above antennae, quite dense below; wings becoming lightly infuscated toward outer margin, veins pale brownish, stigma more piceous, with the usual 3 submarginal cells, the 2nd being quite narrow; tegulae yellowish-hyaline, darker along inner margin; legs piceous, becoming somewhat paler toward apical tarsal segments; scutum coarsely reticulate, scutellum more rugoso-punctate; pleura very coarsely reticulate; dorsal area of propodeum coarsely and irregularly striate, the lateral surfaces somewhat striate below, becoming more finely so above, posterior face coarsely reticulate; abdominal terga smooth and shining, basal segment practically impunctate, 2nd and 3rd terga finely and rather closely punctate over basal half, becoming very sparsely so toward impressed apical margins which are broad and entirely impunctate; gonostyli much exceeding penis valves, with a subtriangular inner ventral lobe and with only a very few short and inconspicuous setae.

HOLOTYPE: Male, Gainesville, Fla., Apr. 25, 1921 (P. W. Fattig) [Cornell Univ.].

In the coarsely reticulate dorsum of the thorax this unique specimen is entirely different from any of the other eastern species of *Sphecodes*.

Sphecodes atlantis sp. nov.

FEMALE.—Length 4 mm.; head and thorax black, abdominal segments 1 and 2 entirely ferruginous, the 3rd becoming darkened apically, following segments piceous; head nearly as long as broad; eyes only very slightly convergent below; clypeus very slightly convex; labrum about as long as broad, quite evenly rounded, yellowish-testaceous except for the somewhat darker base; mandibles quite slender, with a barely discernible inner subapical tooth, color testaceous, becoming ferruginous apically; antennae black basally, becoming brownish apically, basal segment of flagellum shorter than long, about equal in length to pedicel, 2nd segment not much longer, the 3rd and following segments very slightly longer but hardly longer than broad; lateral ocelli slightly nearer each other than to eyes; face below ocelli somewhat shining, the punctures rather fine but deep and distinct, well separated but not sparse, becoming finer and more sparse below, rather close on supraclypeal area, rather coarse but shallow and quite sparse on clypeus, very fine and quite sparse on vertex between eyes and ocelli, margin back of ocelli obscurely roughened; cheeks finely striate posteriorly, rather smooth and subimpunctate along margins of eyes, smooth, shining and impunctate below; wings hyaline with the usual 3 submarginal cells, veins pale testaceous, stigma somewhat more brownish; tegulae testaceous-hyaline; legs piceous but the tarsi pale testaceous; scutum and scutellum shining, obscurely metallic, the punctures fine, well separated over most of scutum, becoming rather close and more obscure anteriorly, those on scutellum very sparse; scutum with a faint, median impressed line anteriorly; pleura rather densely reticulate or coarsely rugose; the hypoepimeral area densely rugose; dorsal area of propodeum rather coarsely reticulate or substriate, lateral faces irregularly striate below, becoming very finely so above, posterior face transversely and irregularly striate; abdominal terga smooth and shining, basal segment entirely impunctate, 2nd and 3rd with a few exceedingly minute punctures scattered across base but becoming practically impunctate toward apical margin, the quite broad, impressed apical areas polished and impunctate.

MALE.—Length 4 mm.; entirely black; head slightly broader than long; eyes somewhat convergent below; clypeus rather narrow, convex, densely pubescent; mandibles dark basally, becoming obscurely reddish-testaceous apically; antennae dark, apical segments of flagellum somewhat more piceous, basal segment considerably broader than long, subequal to pecidel in length, 2nd and following segments slightly longer but hardly as long as broad; lateral ocelli subequally distant from each other and eyes; face below ocelli rather dull, punctures very fine but deep and distinct, uniformly close, those below antennae obscured by the dense white tomentum; vertex between eyes and ocelli more shining, punctures minute and indistinct, margin back of ocelli obscurely roughened, cheeks obscurely and narrowly striate posteriorly, becoming somewhat smoother along margins of eyes, smooth and shining below; wings hyaline, with the usual 3 submarginal cells, veins pale testaceous, the stigma somewhat more brownish; tegulae brownish-hyaline; legs dark but the apical tarsal segments more testaceous; scutum and scutellum quite smooth but rather dull, sparsely punctate, punctures on scutellum somewhat finer than on scutum; pleura, including hypoepimeral area, quite densely but finely rugose; dorsal area of propodeum rather coarsely but irregularly striate, lateral faces rather smooth above, with a few obscure striae below, posterior face obscurely roughened; abdominal terga

smooth and shining, obscurely metallic, basal segments with a few obscure very minute punctures scattered across the middle, 2nd and 3rd with minute, rather evenly distributed punctures across basal half of discs, becoming nearly impunctate toward the narrow impressed apical margins which are entirely impunctate; gonostyli very short and rather robust, not exceeding penis valves, with a hatchet-shaped, more or less excavated, lobe beneath.

HOLOTYPE: Female, Mt. Mitchell, N. C., July 2, 1941 (T. B. Mitchell).

ALLOTYPE: Raleigh, N. C., May 15, 1945 (Mitchell, on *Ceanothus*). PARATYPES: NORTH CAROLINA: 2♀♀, Mt. Mitchell, July 2, 1941; 1♀, Core Point, Beaufort Co., July 17, 1948; 1♂, 1♀, Raleigh, June 7, 1951; 2♂♂, Raleigh, May 15, 1945 (on *Ceanothus*); 1♂, Blue Ridge Pkwy, McDowell Co., June 26, 1952; 1♂, Faison, June 9, 1953 (on celery); 2♂♂, Wayne Co., May 23, 1954 (on *Batodendron*), (all Mitchell); 1♀, Faison, May 2, 1953 (H. & A. Howden); 1♀, Pineola, Aug. 2, 1937 (D. L. Wray) [N. C. Dept. Agr.]; 1♂, Haywood Co., June 17, 1955 (H. V. Weems, Jr., on *Hydrangea arborescens*). MICHIGAN: 3♀♀, 1♂, Midland Co., May 19 & 29, 1945, July 16 & Aug. 26, 1944; 1♀, Mecosta Co., June 25, 1949; 1♂, Clare Co., Sept. 4, 1950 (April or Sept.?) 1♂, Muskegon Co., Aug. 2, 1944; 1♂, E. Lansing, Aug. 19, 1948; 1♂, Leelanau Co., July 5 (all R. R. Dreisbach); 1♂, Otsego Co., July 13, 1923 (T. H. Hubbell) [Univ. Mich.]. GEORGIA: 1♂, White Sulphur Springs, Hall Co., June 6, 1923 (F. W. Walker) [Hubbell]. MASSACHUSETTS: 1♀, Forest Hills, July 17, 1929 [M. C. Z.]. NEW YORK: 1♀, Ithaca, June 9, 1914; 1♂, Ithaca, Aug. 31, 1947 (C. Robinson). ALABAMA: 1♂, Leroy, June 11, 1917. ARKANSAS: 1♂, White River, Aug. 9, 1930 (J. C. Bradley). TENNESSEE: 1♂, Memphis, June 4, 1918. TEXAS: 1♂, Victoria, June 24, 1917 [all Cornell Univ.]. VERMONT: 1♀, Stratton Mts., July 15, 1938 (H. Pratt). MINNESOTA: 1♂, St. Anthony Park, Ramsey Co., Sept. 5, 1924 (Walter Carter); 1♂, Stillwater, July 4, 1940 (M. W. Wing); 1♂, Pine Co., Sept. 25, 1938 (H. S. Milliron); 1♂, University Farm, Ramsey Co., June 22, 1921 (Wm. E. Hoffmann) [all Univ. Minn.]. FLORIDA: 2♀♀, Arcadia, Mar 2, 1954; 1♀, Everglades, Apr. 1, 1953; 1♀, Fort Pierce, Apr. 2, 1954 (all K. V. Krombein) [U. S. N. M.]; 4♂♂, Alachua Co., Apr. 20, May 6, & 13, 1955 (H. V. Weems, Jr.).

The evidence for this association of the sexes is not too conclusive, however; the two apparently occupy the same range, are in flight at the same time, and allowing for sexual differences, they bear some resemblance to each other. A male and a female were collected together at Raleigh, N. C., but whether or not they were mating is not known.

THE GENUS *ANAXIPHA* IN THE UNITED STATES (ORTHOPTERA: GRYLLIDAE)[1]

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The crickets of the genus *Anaxipha* are straw-colored to brown and about five to eight mm. in length. They are very active and commonly inhabit low dense

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plants, but are occasionally found among litter on the ground or in tall shrubs or small trees. Unlike true ground crickets such as *Nemobius*, they are able to walk up the side of a glass jar.

Rehn and Hebard (1912) recognized only two species of *Anaxipha* as inhabiting North America north of the Rio Grande. One was the common, widely distributed *A. exigua* (Say, 1825), which, prior to 1912, was the only species recorded from the United States. The second was *A. pulicaria* (Burmeister, 1838), described from Jamaica. They placed *Cyrtoxipha delicatula* Scudder, 1877, as a synonym of *A. pulicaria*, based on the long-winged form of the species. They also mentioned differences in the shape of the head and pronotum, between *Cyrtoxipha* and *Anaxipha*. They included a key to separate the two species of *Anaxipha*. The characters mentioned included the relative lengths of the hind femur and ovipositor and the proportions of the tympanum in the male tegmen. They also mentioned the longitudinal dark lines on the outer face of the femur in *exigua*.

Hebard (1915) added *A. imitator* (Saussure, 1878) and *A. scia* Hebard, 1915, to the list of species occurring in the United States. Rehn and Hebard (1916) recorded a fifth species, *A. vittata* (Bolivar, 1888). It was characterized by a sharply contrasting color pattern, which Rehn and Hebard (1916) said was weakly indicated in some specimens. Blatchley (1920) reduced *vittata* to the rank of a subspecies, giving, as the main reason, the variation in color pattern. It is well to mention here that certain specimens referable to *pulicaria* at that time, as well as many specimens of *exigua* and *scia*, have dark markings which conform more or less to a common pattern. From 1924 until the present time, most students of the Orthoptera have followed Hebard in recognizing five species in the United States, namely *imitator*, *exigua*, *scia*, *pulicaria*, and *delicatula*, the name *pulicaria* being used for the species previously recognized as *vittata* and the name *delicatula* for species formerly identified as *pulicaria*. The present contribution to the knowledge of *Anaxipha* is the result of an effort to find additional characters by which the several species may be defined. The correct names of some species may be in doubt for years.

The writer's interest in *Anaxipha* began some time after he became a resident of North Carolina in 1928. It soon became evident that there were two species of *Anaxipha* in the vicinity of Raleigh, namely *delicatula* and *exigua*. *Anaxipha delicatula* appears in the adult stage only during early summer, whereas *exigua* is in the adult stage from late July until October or later. Both species occur in some habitats, adults of one following the other with little or no interval between.

Additional species were found in the coastal regions of North Carolina. A species occurring in the salt marshes had a tinkling song very much like that of *exigua*. This species also had an obscure longitudinal stripe on the outer face of the hind femur, like *exigua*. Living or recently killed specimens showed the stripe so plainly that they were placed with *exigua* at first. Later it was noticed that the salt marsh specimens had shorter ovipositors than *exigua*, and that the tarsal claws were smooth whereas those of *exigua* had about three teeth between the middle and the apex. In 1940 the writer had an opportunity to examine the type of *scia* at Philadelphia and was convinced that the cricket in the North Carolina

salt marshes was the same as the type of *scia*. No specimens of *exigua* have been found in North Carolina salt marshes.

In searching for new useful characters for species diagnosis, the writer found that the phallus or male copulatory organ in *Anaxipha* had a very distinct structure in several species. By examination of the phallus of many specimens it was found that there were two species referred to *delicatula* which could be separated in the male sex but not as yet in the female. Dr. A. B. Gurney has determined by examination of the type that the name *delicatula* should be applied to the species with wider distribution in North Carolina. The other species, which is probably new, has been taken only near the coast.

New Characters for Use in Diagnosis

THE HIND FEMUR STRIPE.—This is not a new character but it is one which needs some explanation. In *exigua* and *scia* it is a broad dark stripe with entire unincised margins which runs along the sulcus just below the middle of the outer face of the hind femur. It is most distinct in *exigua* but even in this species a few specimens have a stripe but a little darker than the ground color of the femur. There is some indication that these specimens were in a teneral condition when killed. Another difficulty arises when the muscles inside the femur dry in contact with the cuticle. This produces a reddish brown discoloration which may obscure the natural pattern, especially if it occurs along the sulcus.

Pale specimens of *scia* have a solid femur stripe like that of *exigua*, but in dark specimens the ground color of the femur is often so dark that the stripe is obscured. In *pulicaria* there is a dark net-like pattern on the dorsal part of the outerface of the femur, while above and below the sulcus there may be more or less broken, dark narrow lines with jagged margins, quite different from the solid stripe in *exigua* and *scia*. At its best, the femur stripe is not a good character because it depends on the presence of hind legs, which are easily broken off.

THE TARSAL CLAWS.—All the species except *scia* have prominent teeth on the lower edge of the claw (Fig. 18, 19, 22). All claws on a specimen are similar in structure but usually only one or two are in a good position for examination, or are free of foreign material. The best way to examine the claw is to look at the end of the last tarsal joint, with the line of vision about parallel to that joint. If the background is strongly lighted and the claw itself in shadow, the teeth are easily seen in profile. Dust particles may be removed by careful brushing with a fine-pointed moist brush.

FRINGES ON TIBIAL SPINES.—This character has the same fault as the femur stripe in that it depends on the presence of at least one hind leg. It is a fringe of long hairs on each of the six spines on the distal half of the hind tibia (Fig. 23). The hairs, numbering five to ten, are nearly parallel and in a single line on the side nearest the tibia. Short hairs, but little longer than the diameter of the spine, cover the spine on all sides. Fringe hairs appear to be easily broken, because some specimens have lost nearly all. Even one or two long hairs in the proper place indicate that the fringe was once present. This fringe should not be confused with the combs of hairs on the largest spurs at the distal end of the hind tibiae.

Four species have fringed spines but two do not, so the value of the character is limited.

THE PHALLUS.—The male copulatory organ lies in a horizontal position directly above and concealed by the subgenital plate. In a fresh specimen the phallus can be pulled out by stretching the thin cuticle at the base. The specimen will dry with the phallus exposed. Dry specimens must be relaxed by keeping them in a moist chamber, and by wetting the tip of the abdomen with a small brush. If this fails, the tip of the abdomen may be removed so that the phallus can be dissected under water. It can be kept with the specimen in a drop of glycerin in a minute vial, or attached dry to a paper point.

The function of the whole organ is evidently the same as in other crickets, to mold a spermatophore and insert its tube into the genital organs of the female. Our interest in the phallus is on account of the specific differences in structure shown by it. The partly sclerotized terminal portion of the phallus is about 0.5 mm. long. It has a flattened cylindrical shape, becoming flatter at the free end. The ventral side, in resting position, bears a median groove which holds the tube of the spermatophore when it is formed. The groove lies in a thin, pale sclerite with poorly defined margins, which takes up about half the area of that side of the phallus. Between the median sclerite and the lateral margins, the cuticle is very thin and flexible, and sinks in, causing the whole organ to be much flatter when dry.

On the dorsal side, the cuticle is somewhat more rigid. A dark, sclerotized supporting frame in the shape of the letter H is found in most species. The space between the proximal arms of the frame is occupied by thin cuticle. The distal arms form the lateral supports of the terminal portion of the phallus. Distally they have a pointed or truncated free edge which bears several curved bristles. Between these lateral processes are fleshy terminal lobes which probably are movable in life. In a freshly killed specimen these lobes will tilt on an axis running diagonally from near the midline on the dorsal side to a point on the ventro-lateral side. This capacity for movement is occasionally responsible for some distortion although most of the specimens dry with the terminal lobes in the same position. The terminal lobes are sparsely clothed with minute short hairs. The median groove on the ventral side terminates as a sharp point in the notch where the terminal lobes of the two sides meet. Evidently the terminal lobes have a part in guiding the spermatophore tube to the proper place in the female.

The cross-bar in the H-shaped frame will be called the yoke. Distal to the yoke on the dorsal side between the lateral processes, the cuticle is sparsely clothed with short hairs. Specific differences are found in the shape of the yoke, of the lateral processes and of the terminal lobes. *Anaxipha exigua* and *scia* (Fig. 3–6) are almost alike. The lateral process in *scia* has a longer and more slender point.

The phallus of *A. imitator* has the most distinctive structure (Fig. 1, 2). It is less flattened than in the other species. There is no clearly defined yoke, but distal to the usual location of the yoke there is a prominent swelling about half as wide as the whole phallus. The lateral processes are thin blades with acute

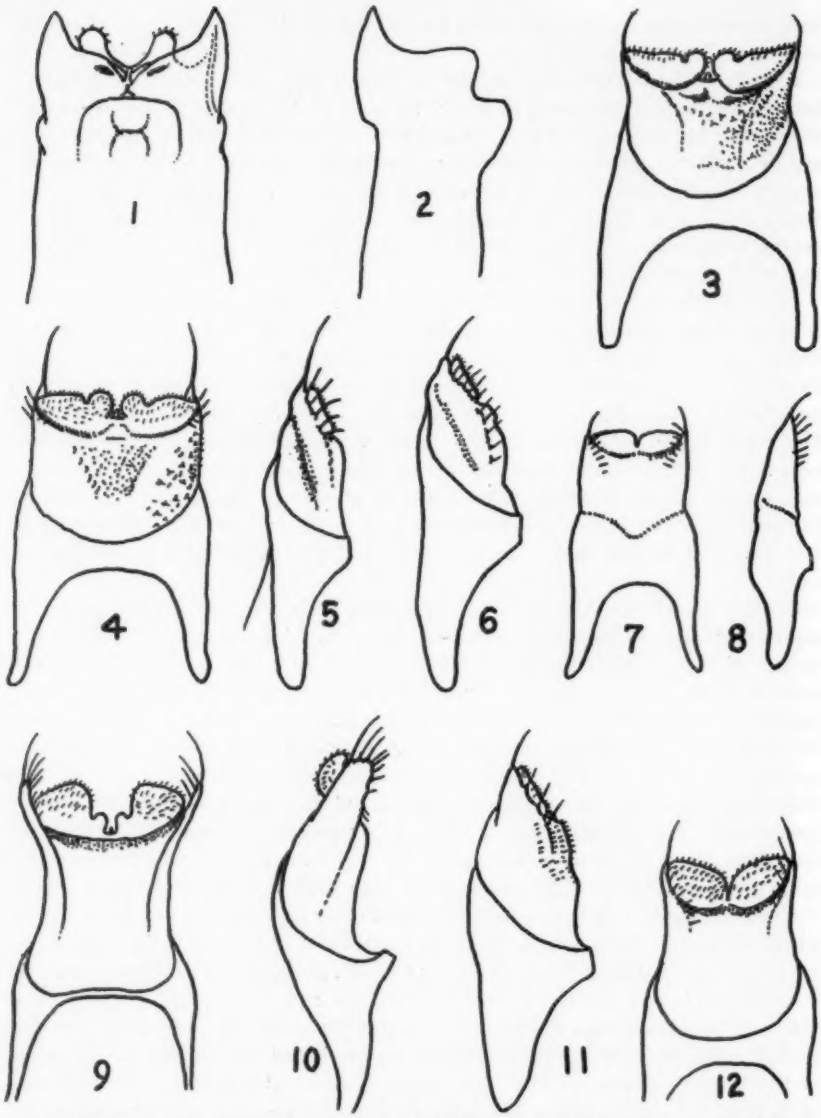

FIG. 1–12. Dorsal and left lateral views of phallus of *Anaxipha*. FIG. 1, 2. *A. imitator*, Matheson Hammock, Fla. FIG. 3, 6. *A. exigua*, Raleigh, N. C. FIG. 4, 5. *A. scia*, Carolina Beach, N. C. FIG. 7, 8. *A. pulicaria*, Gainesville, Fla. FIG. 9, 10. *A. litarena*, Carolina Beach, N. C. FIG. 11, 12. *A. delicatula*, Fayetteville, N. C.

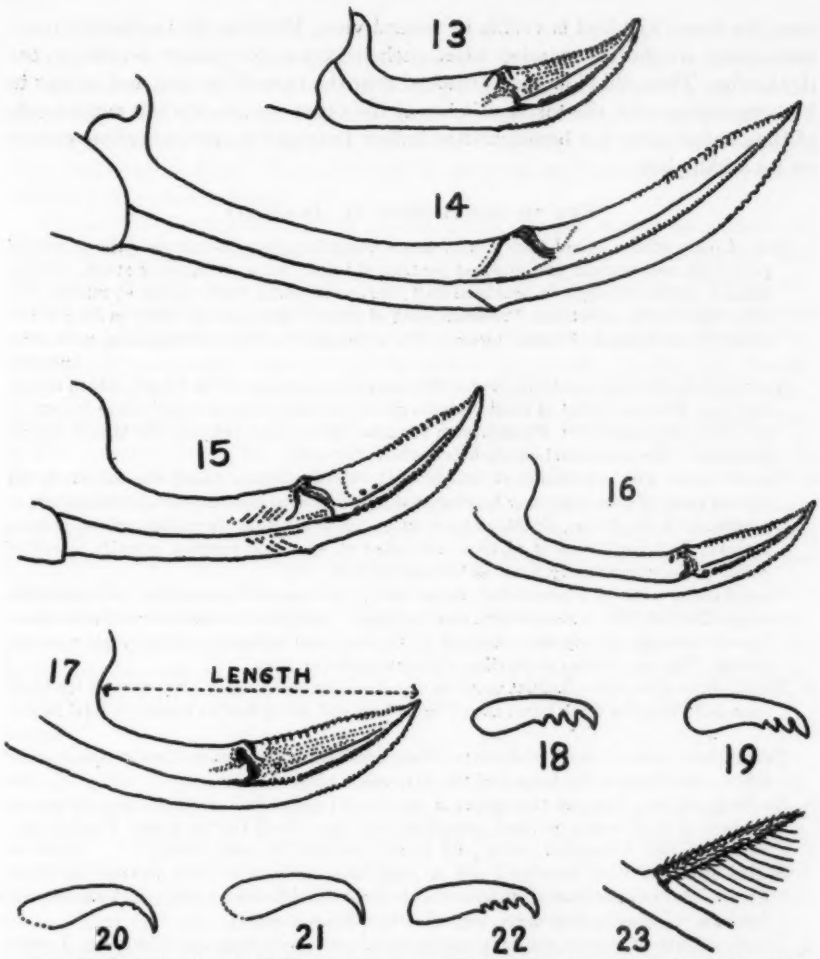

FIG. 13–23. Ovipositors (13–17) and claws (18–22) of caudal tarsi of species of *Anaxipha*. FIG. 13. *A. imitator*. Paradise Key, Dade Co., Fla. FIG. 14. *A. exigua*, Raleigh, N. C. FIG. 15. *A. scia*. Carolina Beach, N. C. FIG. 16. *A. pulicaria*. Warburg Lake, Alachua Co., Fla. FIG. 17. *A. delicatula*. Raleigh, N. C. FIG. 18. *A. exigua*. Gainesville, Fla. FIG. 19. *A. delicatula*. Raleigh, N. C. FIG. 20. *A. scia*. Brickell's Hammock, Miami, Fla. FIG. 21. *A. scia*. Carolina Beach, N. C. FIG. 22. *A. litarena*. Carolina Beach, N. C. FIG. 23. One of the spines of a caudal tibia, showing the fringe of long hairs (*A. scia*).

tips which are oriented in a diagonal direction, being farthest apart on the ventral side. In profile (lateral view) they have the same shape as in ventral or dorsal view. In either case they bear a resemblance to a cat's ears. On the ventro-interal face each lateral process is provided with a thin keel extending from the base to

near the apex. The keel is visible in ventral view. Between the two lateral processes, there are shorter rounded lobes, each having a few minute bristles on the distal edge. These thin lobes are attached near the base of the keel and appear to be homologous with the terminal lobes of the other species. On the ventral side of the phallus there is a broad median hollow bearing the spermatophore groove on its middle line.

KEY TO THE SPECIES OF *ANAXIPHA*

1. Side of body with a broad dark brown stripe extending from eye across lateral field of pronotum and tegmen and exposed portion of folded wing. Ovipositor stout, ventral margin almost straight in proximal half, curved in distal half, widest at middle, decreasing in both directions. Proximal joint of caudal tarsus about twice as long as the other two combined. Phallus terminating in paired structures resembling cat's ears. *imitator*.

   No lateral dark stripe as above. Ovipositor curved for almost entire length, width nearly uniform. Proximal joint of caudal tarsus not more than one and a half times as long as the other two combined. Phallus with terminal fleshy lobes between the tips of lateral processes. The processes bearing bristles near the apex..... 2

2. Caudal femur with a broad dark stripe, with entire margins, along the sulcus on the lateral face. (This stripe may be obscured when general color is dark.) Ovipositor, in profile, with an obtuse, slightly protruding angulation near the middle of the ventral margin. Terminal lobes of phallus truncated at apex and bearing apically a pair of small knobs which nearly touch at the middle line..... 3

   Caudal femur without a broad dark stripe along the sulcus on lateral face but sometimes (in *pulicaria*) with a narrow line having jagged margins or a row of confluent spots. Ventral margin of ovipositor curved all the way and without a slight angle near the middle. Terminal lobes of phallus without knobs at apex..... 4

3. Tarsal claws with three distinct teeth on the disto-ventral margin. Ovipositor with blade (not including the thick base) over 2 mm. long and about half as long as caudal femur. *exigua*

   Tarsal claws without teeth. Ovipositor blade generally under 2 mm. Caudal femur about 2.3 to over 3 times the length of the ovipositor blade..... *scia*

4. No fringe of long hairs on the spines of the caudal tibia. Pale, with sharply delineated pattern of dark brown on head, pronotum and legs. Small for the genus. Phallus thin, wedge-shaped, truncated, with yoke poorly defined but very broad..... *pulicaria*

   Spines of caudal tibia bearing a row of long, thin hairs on the side nearest the tibia. Straw-color to pale brown, with more or less obscured brownish pattern. Yoke of phallus narrow, often dark in color, with clearly-defined margins..... 5

5. Terminal lobes of phallus sub-truncate in dorsal view, with deep notch between. Lateral processes pointed, not exceeding the terminal lobes. Phallus straight in lateral view. No character known for separating female from the next species..... *delicatula*

   Lateral processes of phallus, in dorsal view, curving outward distally and exceeding the terminal lobes, each of which bears a small knob mesad near the base. In lateral view, the phallus bent dorsally at the yoke, the lateral process being rounded or truncate at the apex where it bears several bristles..... *litarena*

A. imitator (Saussure, 1878)

A. imitator has the most distinctive characters of any species of *Anaxipha* occurring in the United States. In addition to the unique shape of both the ovipositor (Fig. 13) and the phallus (Fig. 1, 2), the color pattern is different from that of any other species. The long, dark lateral stripe from the eye to the tip of the folded wings serves to distinguish the species at a glance. In general appear-

ance it comes closest to the macropterous form of *A. pulicaria*, but it differs from that species in having unmarked hind femora. It also resembles *pulicaria* and differs from the other four species in lacking a fringe of long hairs on each of the six caudal tibial spines, as described under the subject of new characters. Only the macropterous phase has been found and it is doubtful if the short-winged form occurs at all. In all other species of the genus in the United States the short-winged forms predominate.

The known distribution of the species in the United States is confined to southern Florida. It was described from Cuba. Hebard (1915) collected it near Miami on sloping ground, covered with a litter of dried leaves, between the jungle of Brickell's Hammock and a red mangrove swamp. The writer has one pair dated March 15, 1915, from Hebard's series taken at that time. The following Florida specimens were lent to the writer: (1) Dade County, Key Largo, Apr. 25, 1937, 1♂, 4♀ (on jungle floor), H. F. Strohecker; (2) Matheson Hammock, near Miami, Nov. 11, 1936, 1♂, H. F. S.; (3) Dade Co., Paradise Key (Royal Palm State Park), Aug. 30–Sept. 1, 1925, 20 adults, T. H. Hubbell; (4) Broward Co., Fort Lauderdale, Sept. 3, 1925, 1 ♀, T. H. H.

Hubbell collected at night with a headlight by sweeping along hammock margins and roads and trails within the hammock. He found that *A. imitator* was abundant in ferns and herbage, and also occurred in shrubs, two to four feet from the ground.

Not much is known about the habits of *A. imitator* but Hebard (1915) mentioned that it was found on the ground, jumping and flying nimbly about. He described the song as a series of short trills lasting one or one and a half, occasionally two, seconds, with normal intervals a little less than a second.

A. exigua (Say, 1825)

This is the largest and most widely distributed of any of the native species. In the field it can be recognized by the clearly marked stripe on the hind femur. This species and *scia* have a slight angulation on the ventral margin of the ovipositor where a diagonal ridge on the ventral blade (first valvula) meets the ventral margin (Fig. 14). It differs from *scia* in the sculpturing on the dorsal blade (third valvula). Both species have, in common with others in the genus, a slight angulation on the dorsal margin, where a shallow diagonal furrow meets the margin. The furrow has a rough surface while the surface on both sides is shiny. The proximal shiny area includes a transverse ridge. In *scia* (Fig. 15), the dorsal end of the ridge meets the furrow, whereas in *exigua* there is a considerable interval between them, and the surrounding shiny area is broader and smoother (Fig. 14).

Anaxipha exigua has the longest ovipositor of any native species in the genus, both in actual length and in relation to the hind femur and the whole body. No specimen examined by the author has an ovipositor under 2 mm., but some are only 2.2 mm. No ovipositor longer than 3.2 has been examined. The length of the caudal femur divided by the ovipositor length gives a number close to 2, with a range of 1.87 to 2.27. The ovipositor, as here measured, includes only the blade, measured on a straight line (see Fig. 17). The body, excluding the ovipositor, is

generally not more than a millimeter longer than the hind femur, in dry specimens.

Anaxipha exigua is the only species of the genus to be found over much of the eastern half of the United States. Rehn and Hebard (1912) looked up original charts and found that the type locality for *exigua*, usually given as Missouri, was actually 80 miles west of Kansas City, in Kansas. This would place it very close to the present western limit of distribution of the species. Blatchley (1920) gives the known range of *exigua* as "from southern New England west to Minnesota and Nebraska and south and southwest to Jacksonville, Florida and Brownsville, Texas." Hebard (1925, 1931, 1932) named a number of limital localities extending slightly the known range. Cantrall (1943) found the species in Livingston County in southeastern Michigan. Walker and Urquhart (1940) collected it in extreme southern Ontario near Lake Erie, mostly from a marsh on Point Pelee.

In the collection of the University of Michigan Museum of Zoology, *A. exigua* is represented from only five Florida counties, all of them within a hundred miles of the northern boundary of Florida. Other parts of Florida have been thoroughly collected for Orthoptera. If the species occurred farther south it probably would have been collected there.

Anaxipha exigua has not been collected nor has its song been identified in the higher parts of the Blue Ridge and westward in North Carolina. The species probably occurs in all other parts of the state.

Anaxipha exigua occurs in the adult stage in late summer, in both the southern and northern parts of its range.

In the north, *A. exigua* probably is eliminated or reduced in numbers by early frost. In southeastern Michigan, Cantrall (1943) says that the species is gone by late September. In the south the species is often present until late November.

HABITAT.—*A. exigua* has been collected from quite a variety of habitats, but most of them have one or two features in common. They are low, moist places or dense thickets, or both. Blatchley (1920) states that in northern Indiana it is found among the sphagnum mosses growing in dense tamarack swamps and also on the shrubs about the margins of lakes and marshes. He also states that farther south it is often very abundant on the leaves and stems of arrow arum, cat-tail flags, button bush and other semi-aquatic plants. On the George Reserve in southeastern Michigan, Cantrall (1943) states that *A. exigua* is characteristic of the wet shrub zone, and is invariably seen or heard on shrubby plants, its favorite being button bush (*Cephalanthus occidentalis* L.).

The unpublished collecting notes of T. H. Hubbell contain descriptions of habitats where *A. exigua* was collected as follows: (1) woods bordering a river, (2) cane brake vegetation on slopes of a gully, (3) thick herbage on marshy valley floor, (4) tall weeds on gravel bar and sand banks, (5) willow-blackberry-herbage thickets along stream, (6) swamp forest flood plain, the wetter areas covered with *Saururus* and other succulent herbs, forming stands about two feet tall, (7) dead leaves in bottom of ravine.

In his ecological study of the Welaka area in Putnam County, Fla., Friauf

(1953) found *A. exigua* in only three types of habitat, but it was "abundant" in all three, when present at all. They were designated as follows: (1) moist ruderal grassland, (2) bayhead, (3) alluvial hammock, or river swamp. *Anaxipha exigua* was found in the herbage or shrub stratum.

SONG TYPES AND HABITATS OF *A. EXIGUA* IN NORTH CAROLINA.—A very puzzling situation exists with regard to the local distribution of song types. The writer learned to recognize, during his first year in North Carolina, three types of cricket songs, which, when traced to the singer, proved to be those of *Anaxipha exigua*. The three songs were named some years later in a publication by the writer (1951) as follows: (1) slow tinkle, (2) fast tinkle, and (3) trill. Each song is apparently produced as a series of sound pulses, each pulse made by a single movement of the tegmina and resulting in a sharp chirp. The main difference between the song types is in the frequency of the chirps which in all three types is influenced in a similar manner by temperature. In the slow tinkle the chirps are slow enough to count, except possibly on hot summer days. On cool mornings, at temperatures of 60 to 65°F. there are 3 to 3.5 chirps per second, and at 70 to 75°F. there are 4 to 5 per second.

The fast tinkle is too fast to count even at 60 to 65°F., when the chirp frequency is about 7 to 8 per second. At 75°F. the fast tinkle has an estimated frequency of 11 chirps per second. At this rate or faster the song still has a tinkling quality. The slow tinkle at high temperature approaches the fast tinkle at low temperature. The trill at first appears to be a continuous prolonged sound, but on careful listening it is found also to be a series of discrete chirps, but of such high frequency that it is impossible to estimate the number per second. When a trilling male starts to sing after being disturbed it sometimes trills in short trains of sound of one or two seconds' duration before starting a continuous trill.

For timing chirp rates too fast to count, the writer made use of a crude instrument for producing tapping sounds at different rates which could be compared in the field with cricket songs. The instrument consisted of a piece of thin, flat steel spring about a foot long, weighted with lead at one end and clamped between blocks of wood at the other end. By shifting the level of the spring between the blocks, the spring could be made to swing at rates varying from three to five per second. With a little practice it was found possible to shake the whole device in such a way as to keep the spring swinging at a fairly uniform rate. Two brass arms could be adjusted so that the spring would tap lightly against one arm at one end of each swing, or both arms at opposite ends of the swing. The instrument was taken to the field with the latter adjustment and the length of the swinging end was varied until the frequency of taps simulated the chirp frequency of the fast tinkle song under observation. One arm was then moved away until the slower tapping rate was counted. The chirping rate of the cricket was twice as fast as the reduced tapping rate. This device made it possible to estimate chirping rates up to ten per second or a little faster.

The determination of chirp frequency with this device may be slightly inaccurate but there is no doubt about the existence of three song types in the species.

The greatest chance of error is in confusion with other species of *Anaxipha* or with certain species of *Nemobius*. The slow tinkle is very much like the song of *Nemobius fasciatus tinnulus*, which is a series of discrete chirps at a slightly higher frequency. The song of *N. f. fasciatus* has a chirp frequency a little faster than the fast tinkle of *A. exigua*. The trill of *A. exigua* resembles the trilling song of certain species of both *Anaxipha* and *Nemobius*. The songs of *A. exigua*, slow tinkle and fast tinkle, are clearer, more bell-like, and maintain an even more constant rhythm than the rhythmical *Nemobius* songs they are compared with above.

The two tinkling songs of *A. exigua* together constitute one of the commonest elements of the cricket chorus to be heard in late summer and fall, especially in the piedmont area of North Carolina. In the mountain region, no song that could be identified as one of the tinkling songs of *A. exigua* has been heard, except on the lower foothills of the Blue Ridge, where the fast tinkle song and the cricket producing it have been identified. In the higher parts of the mountains the recognition of the fast tinkle is made difficult by its resemblance to the song of *Nemobius fasciatus fasciatus*, which is heard singing wherever grass grows in the mountains.

A few observations were made on the daily song period of the two tinkling races of *exigua*. Like many species of crickets they can be heard both in daylight and in dark and are most commonly silent during the hot parts of the day. A few start singing in the late afternoon and evening, and more after dark, but it is not until morning again that the full chorus is singing.

Allard (1910) described the song of *A. exigua* in northern Georgia as a shrill, prolonged, tinkling "ti-ti-ti-ti-ti-ti." Cantrall (1943) described the song in southern Michigan in the same manner. These descriptions evidently apply to one of the tinkling songs, but since there is no mention of frequency they could refer to either the slow or the fast tinkle. In North Carolina both songs are heard in the same places but the fast tinkle usually outnumbers the slow tinkle. They occur in woody thickets in sunny situations, both upland and lowland. The two songs are found less commonly among tall weeds than in blackberry briars, young trees, shrubs, vines and other woody plants growing along forest borders, roadsides, ditches and small unshaded streams. They are also heard about dwellings, in ornamental shrubs and hedges. A pure population of crickets producing either the fast or slow tinkle has not been found, except for very small areas, such as a clump of bushes. No habitat has been found in which one form is regularly present and the other absent.

The writer has sometimes listened to one individual cricket for many minutes without hearing it change its song. He has also kept a male of one song type or the other with a female in a jar where the song could be heard frequently. No shift to one song type from another has ever been observed. It is probable that each male is capable of producing only one kind of song. The relation of the slow tinkle to the fast tinkle is still an unsolved problem. It could be a case of dimorphism for a song type. A solution of the problem by crossing experiments would encounter serious practical difficulties. The collection of the crickets from

woody thickets is very difficult and there is no way of identifying the females as to song type. Another difficulty would appear in the care of the eggs, because there is only one generation per year and the eggs would need to be kept viable over winter in the pithy plant stems where they are deposited.

The habitat distribution of the race producing the trilling song of *A. exigua* is entirely different from that of the two tinkling songs. The trilling race prefers deep shade rather than sunlight. The song was first heard by the writer in a deep, shaded ravine near Raleigh, N. C., where the song was traced to the singer on the ground among dead leaves. Later, the race was found along other wooded valleys and on plants growing in water and wet ground on the shaded banks of an old mill pond. The trilling race was found in greatest abundance in small patches of marshy ground, completely shaded and subject to flooding, in alluvial deposits along a small creek. In such places it was found largely on a plant called Lizard's tail, *Saururus cernuus* L., which grows about two feet high. Sometimes the crickets became so abundant that a few sweeps of the net through the tops of the Lizard's tail caught as many as five at one time. The combined singing of so many males filled the air with a shrill ringing sound. In the Lizard's tail marshes the crickets were living on the tops of the plants, as indicated by the ease with which they were collected by sweeping. In the wooded valleys many of the crickets were found among the dead leaves on the ground or on low plants a few inches from the ground. One was traced by its song to an alder leaf over six feet above ground.

Two of the three types of stridulation by *Anaxipha exigua* heard in North Carolina are also known to occur in Ohio, where they have been studied by Edward S. Thomas of the Ohio State Museum. His observations are summarized here from unpublished information. He says that the trill is heard abundantly in low ground throughout Ohio, where the song is produced by a large race of *A. exigua*. The other song, which is a fast tinkle like the song of *Nemobius fasciatus*, is produced by a smaller race of *A. exigua*. It is heard in hot dry uplands, usually associated with pines. It is also heard in leaf litter on the ground, and in all kinds of shrubbery. It has not been found north of Sugar Grove, Fairfield County, Ohio. Thomas found no significant difference in the male genitalia of the two forms but thinks they could be separated on the basis of size alone. Specimens of both races have well-marked femur stripes and females of both have a distinct angulation on the ventral margin of the ovipositor. Thomas has never found in Ohio the third type of *A. exigua* song, the slow tinkle, but he claims to have heard it at low altitudes near Gatlinburg, Tennessee.

A. scia Hebard, 1915

This species and *exigua* have some features in common, such as the dark femur stripe and the general shape of the phallus (Fig. 4, 5). The phallus of *scia* has the lateral process tapering to a more accuminate point than in *exigua*. The ovipositor in both species (Fig. 14, 15) has a very slight angulation in the ventral margin near the middle as seen in profile, differing in this respect from the other species except *imitator*. The ventral angulation is more distinct in *exigua* and

the sculpturing near the middle of the dorsal component of the ovipositor differs in *scia* and *exigua*, as shown in the drawings and explained under *exigua*. No ovipositor, in specimens identified as *scia*, has been found as long as 2.0 mm., but ovipositors as long as 1.7 mm. and 1.8 mm. are fairly common.

The most unique character of *scia* is the shape of the tarsal claws (Fig. 21), which are long, curved and smooth whereas the other species of *Anaxipha* have a row of three or four teeth on the disto-ventral side. Unfortunately, one to three very small teeth have been found in a few specimens (Fig. 20) that agree with *scia* in other respects. The color of *scia* is generally a medium brown with the head and pronotum a little darker than the tegmina. Florida specimens seem to average a little darker than North Carolina specimens.

The female type of *scia* and the male allotype were collected by Hebard among tidal litter in a mangrove swamp at the edge of Brickell's hammock, Miami, Fla., on March 16 and 15, 1915. No other adult specimens were collected at that time, but the writer has one female and two male specimens bearing Hebard's label showing that they were collected at the same place on March 8, 1919. The writer examined and measured the type and allotype in 1940. His measurements generally agree with Hebard's (1915) published description, except in the length of the ovipositor, which was found to measure 1.85 mm. in the type whereas the published description gave 2.7 mm., a length which is entirely out of line with other specimens. A possible explanation is that the thick basal portion might have been included in Hebard's measurement, rather than the blade alone as measured by the writer (see dotted line, Fig. 17).

The length of the hind femur divided by the length of the ovipositor gives a higher number in *scia* than in *exigua*. Some sample specimens of *scia* gave measurements as follows:

Series	Ovipositor	Femur Divided by Ovipositor
Miami, Fla., March 16, 1915 (type)	1.85	2.3
Miami, Fla., March 8, 1919	1.7	2.4
Cortez Beach, Fla., Jan. 4, 1925	1.65	2.5
Cedar Keys, Fla., July 12, 1925	1.7	2.7
Carolina Beach, N. C., Sept. 14, 1932	1.75	2.9
Carolina Beach, N. C., Sept. 14, 1932	1.82	3.0
New Bern, N. C., Aug. 27, 1946	1.72	2.9
New Bern, N. C., Aug. 27, 1946	1.8	3.3
Amargosa Desert, Nev., Aug. 23, 1919	1.85	2.6

Additional information on the habits and distribution of *A. scia* has been obtained from the field notes of several collectors of this little known species. The unpublished notes are summarized by states as follows:

Florida: MANATEE CO.: Cortez Beach, Jan. 4, 1925, 4♂, 3♀, T. H. Hubbell; collected at night by beating young mangrove seedlings and other vegetation growing in chamber-like openings roofed by mangrove branches. LEVY CO.: Cedar Keys, July 12, 1925, 10♂, 2♀, T .H. H.; collected at night with headlight in shoreward margins of salt marsh on northeast side of Cedar Key, by trampling clumps of reeds into the muck and looking for crickets to crawl out. **South Carolina:** GEORGETOWN CO.: Georgetown, Aug. 17, 1931, 1♂, macropterous, S. B.

Rochester. **North Carolina:** NEW HANOVER CO.: Carolina Beach, Sept. 12, 1928, 1♂, 1♀, Fulton. Sept. 14, 1932, 23♂, 17♀, Fulton. Aug. 30, 1939, 4♂, 7♀, Fulton; in salt marsh, tall grass and rushes. CRAVEN CO.: New Bern, Aug. 27, 1946, 17♂, 16♀, Fulton; tall grass at water's edge. HYDE CO.: Swanquarter, Aug. 11, 1953, 4♂, W. M. KULASH; macropterous, at light, near a large salt marsh. **Virginia:** Tappahannock, Sept. 9, 1915, 1♀, Hebard. **New Jersey:** Mullica River near New Gretna, August 24, 1924, Hebard; salt marsh. **Nevada:** Amargosa Desert, Fairbanks Ranch, Ash Meadows, August 23, 1919, 1♂, 2♀, Hebard. Further information on this remarkable series is quoted from a letter by Hebard which reads as follows: "The crickets were found in a large colony in Tules (the western bull rush) around a large pool of strongly alkaline water. Individuals were near the surface of the water where the males were keeping up a continuous trilling, more liquid and higher pitch than all of *Nemobius*. Three individuals were taken after long search. . . . They seek the thickest grasses and can be driven into the open . . . only with the greatest difficulty."

From the assembled data it is evident that *scia* is found mainly in two habitats, mangrove swamp and salt marsh. The species is definitely distributed along the coast and is probably confined to tidewater. At present the recorded distribution is from Miami, Fla., to Mullica River, N. J., on the Atlantic Coast, and at Cedar Key and Cortez Beach on the Gulf Coast. The species should occur in salt marshes along the Gulf from Florida to Texas, but so far as the writer is aware no specimens have been collected west of Cedar Key, except the remarkable series from Nevada far to the west of even the widespread *A. exigua*. The habitat is probably not very different from the salt marshes along the Atlantic Coast. The interesting question is how this species got started in such an isolated place.

The three Nevada specimens agree with specimens of *scia* from the east in all known characters except general color, which is very pale in the Nevada specimens. They have very conspicuous stripes on the hind femora, the claws are toothless, the ovipositor is a little less than 2 mm. long and has the slight angulation on the ventral margin, and the phallus is similar to that of eastern specimens of the species.

In Florida, *scia* has been found in the adult stage in January, March, July and September. In North Carolina, *scia* has been found as adults in every month from July to October, inclusive, but has not been seen or heard at other times.

The stridulation of *scia* in North Carolina results in a rapid tinkling, like little bells, very much like the tinkling songs of *A. exigua*. It is a rhythmical repetition of pulses of sound at a high frequency. It has not been possible to compare out-of-doors the songs of *scia* and *exigua*, because the two species are seldom found in the same place.

The writer believes that the pulse frequency of *scia* lies between the slow tinkle and the fast tinkle of *exigua* as described under that species. At temperatures between 60°F. and 65°F. the slow tinkle of *exigua* has 3–4 pulses per second, *scia* 4–5, and the fast tinkle of *exigua* is estimated at 7–9 pulses per second. Thus the song of *scia* is similar to the song of *Nemobius fasciatus tinnulus*, which never occurs in the same habitat with *scia*. *Anaxipha scia*, like *exigua*, sings most vigorously in the morning, and very little on cool nights.

A. pulicaria (Burmeister, 1838)

After studying a large number of specimens in the Philadelphia collections from the West Indies, and Central and South America, Hebard (1924) concluded that the name *A. pulicaria* should be used for the species which Rehn and Hebard (1916) recognized and discussed as *A. vittata*. Hebard (1924) pointed out that the name *A. delicatula* (Scudder, 1877) was available for the species which previously had been determined as *A. pulicaria*. He also stated that Bolivar's *vittata* may be a synonym of *pulicaria*, the description of *vittata* being based on West Indian material and of such a character that definite assignment can not be made without examination of the type.

The species now recognized as *pulicaria* can be identified by several characters. The structure of the phallus is probably the most dependable character (Fig. 7, 8). It is flatter than in other species and tapers to a thin, wedge-shaped truncated tip. In some specimens the phallus becomes warped on drying and results in a trough-shaped organ. The yoke is unpigmented, very broad (as measured along the middle line) and has poorly defined boundaries. The spines on the hind tibiae lack a row of long hairs on the side nearest the tibia. The fringe is present in all the other native species of *Anaxipha* except *imitator*. The presence of the fringe can be taken to indicate that the specimen is not *pulicaria* or *imitator*. The absence of all fringe hairs could indicate that they have been broken off, in which case the identification must be based on other characters. The same is true if both hind legs are missing. The ovipositor (Fig. 16) is short, pale and narrow, usually measuring about 1.3 mm. in length and 0.2 mm. in width.

The body is pale straw-color with a dark brown sharply contrasting pattern on the head, pronotum and legs. The pronotum has a dark pattern on the median area of the disk and on the upper half of the lateral lobes. The hind femur has many diagonal, elongated, brown spots, which in some specimens are united to form one or more jagged lines. The size is usually very small, probably smaller than any species except *imitator*; in fact, the several macropterous individuals of *pulicaria*, in the collections examined, bear a strong superficial resemblance to *imitator*.

Fifty specimens from the University of Michigan Museum of Zoology were examined. All of them were from Florida, taken by several collectors, including T. H. Hubbell, Fred W. Walker, H. L. Speer, and J. J. Friauf. Most of these specimens were collected in Alachua County, around Gainesville or Levy Warburg Lake. Other Florida specimens were taken in Marion County at Ocala National Forest and in Putnam County at Welaka. The dates represented include March, April, June, July and August. Five of the fifty specimens are macropterous.

Unpublished collecting notes by Hubbell give some information on the habitats where the species is found: (1) sweeping tall dry grass, hillside pasture, at night; (2) sweeping herbaceous undergrowth in high hammock, at night; (3) sweeping lush herbage in margins of hammock at dusk.

Only one specimen from a locality outside Florida has been seen by the writer, a single male specimen which he collected at Edisto Beach, S. C., on August 31,

1949, by sweeping grass about a foot high in a flat sandy area on the land side of the first dune, near the beach.

Rehn and Hebard (1916) listed four specimens under the name *A. vittata* (Bolivar). These specimens, which should now be identified as *A. pulicaria*, are as follows: Albany, Ga., Aug. 1, 1913, 1 ♀; Atlantic Beach, Fla., Aug. 24, 1911, 1 ♂; Punta Gorda, Fla., 1 ♀; Key West, Fla., Mar. 15, 1910, 1 ♀.

A. delicatula (Scudder, 1877)

When Hebard (1924) found that the name *A. delicatula* (Scudder, 1877) was available for the species previously identified as *A. pulicaria*, he was not aware that two species were involved. Several years later, the writer compared the structures of the phallus of the species of *Anaxipha* represented in his collection. The males, identified as *delicatula*, were found to be of two species, but the females appeared to be all of the same species. Until better female characters are found, the females will have to be identified by being associated with a series of males of one of the two species, or by being collected in a habitat or geographical area inhabited by only one of the two species.

The immediate problem was to determine which of the two species was *A. delicatula*. Fortunately, Scudder's type was still in good condition and on loan to the U. S. National Museum from the Museum of Comparative Zoology at Cambridge, Mass., where the type is at present located. Dr. A. B. Gurney relaxed the type and made it possible to see the phallus, which was found to be of the short straight form shown in Fig. 11 and Fig. 12. Scudder's description of *Cyrtoxipha delicatula* was based on a macropterous male specimen collected in Florida by J. H. Comstock. Following the description, Scudder wrote, "one male, Fort Reed, April 23. I have also received a male of the same species from Sand Point, Florida, collected May 1, by Hubbard and Schwartz." This comment by Scudder gives the impression that the Sand Point specimen might have been received after the description had been written. This specimen apparently has been lost or destroyed. At any rate the Fort Reed type serves to fix the name *delicatula* for the species having the straight phallus and wider distribution. The other species, which runs through the key to the last couplet, is described by the writer as a new species, *A. litarena*.

Scudder placed his *delicatula* as a species of *Cyrtoxipha* on account of the long wings which are now known to occur as a phase in a small proportion of every short-winged species of *Anaxipha* found in the United States. The macropterous forms are commonly found attracted to lights at night.

Anaxipha delicatula is the only species other than *A. exigua* found as far inland, in North Carolina, as Raleigh, Fayetteville and Hamlet. The Fulton collection also has a macropterous female taken in a trap light at Clemson College, S. C., June 21, 1931, by O. L. Cartwright.

The species has been collected in the adult stage in eastern piedmont North Carolina from May 22 to July 21. During most of this period *A. exigua* occurs only as nymphs. Often the two species are found in the same habitat but not in the same stage. *Anaxipha delicatula* occurs in the piedmont and coastal plain, in

marshes and stream borders, especially in those having large tufts of marsh grasses or a cover of Lizard's tail (*Saururus*). The writer has also a series of four male and five female specimens from the salt marsh at Carolina Beach, collected June 12, 1930.

Other specimens supplying data on the seasonal history or geographic range of the species include the following:

Florida: DADE CO.: Jacksonville, Sept. 19, 1927, 1♂, J. S. Rogers. July 30, 1942, 1♂, R. C. Barnes. Paradise Key, April 7, 1951, 1♂, 3♀, H. and A. Howden; these 4 specimens taken at a light, all macropterous, the females tentatively identified by association with the male. LIBERTY CO.: Hosford, March 21–24, 1954, 32 adults, T. H. Hubbell; perhaps a new species or race. **Louisiana:** New Orleans, June 9, 1923, 2♂, T. H. Hubbell; damaged specimens. **Illinois:** Giant City State Park, June 15, 1955, 1♂, 1♀, R. D. Alexander.

The total range of the species in the United States is from the southern tip of Florida, north to Clemson College, S. C., Hamlet and Raleigh, N. C., and west to New Orleans, La. There is evidence to show that the species probably occurs in northern Virginia in the vicinity of the District of Columbia. Allard (1930) reported the occurrence in this area of a species singing in marshy places in May. This he identified as *pulicaria*, but it seems very improbable that this was the species identified as *pulicaria* by Hebard (1924). Allard's descriptions of the song, habitat, and seasonal history all point to *delicatula* as the probable species.

The crickets collected by Alexander in southern Illinois extend the known range of the species about 500 miles up the Mississippi, if further study does not show them to be a new species. Examination of the crickets showed agreement with *delicatula* in most of the characters found in the genus, including the structure of the phallus, which was dissected out and glued to a paper point by E. S. Thomas. The time of year in the adult stage also points to *delicatula*. The song, as observed by Alexander, is essentially the same as the song of *delicatula* described in this paper. Alexander first heard the song among *Andropogon* in a dry hillside prairie about a hundred yards above a swale, but it was much more common in marshes on cat-tail (*Typha*) or other marsh plants. He heard the song near Cairo, Wolf Lake, Makanda and Carbondale, all in southern Illinois. At two places, Wolf Lake and Carbondale, the song was traced to an individual singer. Four males and two females were collected at Giant City State Park and one male at Carbondale. They were kept alive for observations on the song. During the trip home, all but one male and one female disappeared. There seems to be little doubt, however, that they were all of the same species, *A. delicatula*.

The Illinois crickets differ from specimens of *delicatula* in their brown color, but other series collected near Raleigh, N. C., in early summer, approach this condition. The specimens collected by Hubbell in Liberty County, Fla., are even darker brown. An examination of the phallus of one specimen showed close relationship to *delicatula*, but further study will be necessary before the status of these specimens can be finally determined. Alexander suggests that the brown color of the Illinois specimens might be abnormal, owing to the high humidity at the time they were pinned. Some other insect specimens collected at the same time turned black on account of slow drying.

The song of *A. delicatula* as observed near Raleigh, N. C., is a high-pitched prolonged trill with tonal qualities of *Oecanthus nigricornis*, but weaker, like *Nemobius cubensis*. Sometimes the trill is broken into shorter phrases or trains of three or four seconds' duration with brief breaks between. Some individuals start singing after being disturbed, with phrases shorter than one second before resuming the continuous trill. Others start with a continuous trill, which seems to be the normal calling song when the crickets are undisturbed.

Anaxipha litarena[2] sp. nov.

MALE.—Size and form about average for the genus. Body about 6 mm. long or 6.8 mm. including the tegmina. Head width at eyes, 1.6 mm.; length, vertex to occiput, 1.0 mm. Length of eyes, 0.66 mm. Length of first antennal segment, 0.4 mm. Occiput with small scattered bristles; head between the eyes with a few inwardly curved bristles, below which the number of larger bristles increases, those near the middle line forming a double row, diverging between the antennae. Face below antennae with few small bristles. Terminal segment of maxillary palpi flattened in form of isosceles triangle; apical side slightly shorter than the other two. Pronotum (in dorsal view) width of anterior margin, 1.3 mm.; posterior margin, 1.65 mm. Right tegmen, width of dorsal field, 2.3 mm.; length, 4.7 mm.; depth of lateral field, 0.9 mm. Tympanum of tegmen, length, 2.3 mm.; width, 1.4 mm.; dimensions of inner oval, 2.1 × 1.0 mm. No wing visible. Hind femur length 4.5 mm.; maximum width, 1.2 mm.

Length of tarsal joints

	Proximal	Joints 2 and 3 Combined
Front leg	0.5 mm.	0.66 mm.
Middle leg	0.4 mm.	0.66 mm.
Hind leg	0.8 mm.	0.7 mm.

Length of hind tibia to base of large spur, 4.0 mm. Length of proximal portion to base of proximal spine, 2.0 mm. Length of the 3 external spines on right hind tibia: proximal, 0.56 mm.; middle, 0.60 mm.; distal, 0.56 mm. Interspace to next spine in same row: proximal, 0.56 mm., middle, 0.5 mm.; distal, 0.66 mm. (to spur). Tibial spines with a maximum of 6 long fringe hairs on the side next to the tibia. Hind tarsal claws with 2 or 3 small teeth on the distroventral margin. Anterior tibiae with a sensory tympanum on the caudal face only.

Supporting structure of phallus (Fig. 9, 10) in the usual H-form. Distal half bent dorsad just distad to the yoke. Distal portion constricted beyond yoke, lateral processes then bent strongly outward, then curving inward again so as to lie parallel at the apex, which is the widest part of phallus beyond the yoke. Tips of lateral processes (brown) exceeding the terminal lobes (white). Each terminal lobe with a large distal portion and a small knob-like proximal portion. The distal portions widely spaced, the proximal knobs narrowly separated at the base of the notch. The free tips of the lateral processes truncated and bearing several bristles on the apex and dorsal margin. The terminal lobes bearing scattered short hairs.

COLOR.—Body a pale buff or straw-color. Face without a dark pattern; below antennae, paler; above antennae, with small dark spots where bristles are or were attached. A narrow pale median line extending from vertex to occiput. Pronotum with pale lateral lobes, dorsal area slightly brown with pale,

[2] From *litus* (shore) and *arena* (sand).

narrow, median line. Hind femur straw-color, with a light reddish brown pattern on the upper half, the darker color in diagonal streaks enclosing elongated pale spots. No dark stripe at the sulcus. Abdomen brown on the sides and venter but with a pale stripe on the mid ventral line.

HOLOTYPE.—Male, Carolina Beach, New Hanover Co., N. C. Collected by the author, June 12, 1930, on a shrub, *Iva*, growing on the first dune near the ocean. To be deposited in the U. S. National Museum.

PARATYPES.—Paratypes listed below include only male specimens in which the phallus has been pulled out to make it visible. No allotype or female paratypes have been designated because no female characters are known for distinguishing the species from *delicatula*. Numbers in parentheses, following locality and date, refer to the number of paratypes in each series.

Fulton collection.—**North Carolina:** Carolina Beach, June 12, 1930, (2); April 20, 1930, (4); Sept. 11, 1931, (1); Aug. 31, 1939, (8); Harkers Island, June 11, 1931, (4); Lake Mattamuskeet, July 29, 1946, (2) (1 macropterous). **Florida:** Panama City Beach, Sept. 4, 1949, (3). **South Carolina:** Cherry Grove Beach, July 31, 1936, (4).

University of Michigan Museum of Zoology.—**Florida:** ALACHUA CO.: April 12, 1924, F. W. W. (8); Aug. 24, 1924, F. W. W. (1); April 21, 1924, F. W. W. (1); Aug. 5, 1924, F. W. W. (2); April 5, 1924, F. W. W. (2), March 13, 1924, T. H. H. (1); April 11, 1925, T . H. H. (1); May 3, 1924, T. H. H. (1); March 4, 1925, T. H. H. (1); April 2, 1925, T. H. H. (1); April 1930, T. H. H. (1). COLUMBIA CO.: July 22, 1925, T. H. H. (3). GADSDEN CO.: River Jtc., July 25, 1925, T. H. H. (1). LEON CO.: Tallahassee, April 23, 1924, T. H. H. (1). LEVY CO.: Cedar Keys, Oct. 18, 1924, F. W. W., T. H. H. (3). LIBERTY CO.: Old Camp Torreya, April 27, 1924, and July 27, 1925, T. H. H. (2). MADISON CO.: Ellaville, April 22, 1924, T. H. H. (4). MARION CO.: Juniper Springs, Sept. 4, 1938, and Sept. 9, 1938, H. and F. (2). MARION CO.: Micanopy, April 4, 1926, T. H. H. (2). OKALOOSA CO.: Delaco, Aug. 11, 12, 1935, T. H. H. (1). **Louisiana:** Mandeville, Feb. 25, 1923, T. H. H. (4). **Georgia:** Macon, June 3, 1928, F. W. W. (1).

F. W. W. = F. W. Walker T. H. H. = T. H. Hubbell H. and F. = Hubbell and Friauf

The paratypic series shows a little variation in size. The length to the tip of the tegmen shows a range from about 4.5 to nearly 7 mm. The general color is pale brown with some darker stippling and in some series a slightly obscured dark pattern on the head and pronotum is present. This pattern was more prominent in the series from Harkers Island, N. C., and the sand ridge near Carolina Beach, N. C. There is also some variation in the phallus which may be partly a matter of the form it takes on drying. In some specimens the lateral processes extend beyond the terminal lobes but in others the two parts terminate at about the same level. The truncated tips of the lateral processes may be narrow or broad. The terminal lobes are probably the parts most subject to distortion on drying. The size of the teeth on the tarsal claws is variable but no specimen has been found entirely devoid of teeth.

NOTES ON HABITAT.—The species has a wide range in habitats. At Carolina Beach, N. C., it was first found in April, 1930, in undergrowth on a dry sand ridge. In June and September it was beaten from shrubs on the dunes near the ocean. On August 30, 1939, a good series was taken in the salt marsh. At Lake Mattamuskeet, N. C., and at Panama City Beach, Fla., it was collected from tall grasses growing in water and on the shore.

A wide range of habitats is also shown by specimens collected in Florida by

T. H. Hubbell and F. W. Walker. The small size of the series collected there suggests that the species was seldom very abundant or that it was hard to capture. The largest Florida series was collected by Walker at Warburg Lake, Alachua Co., April 12, 1924, by sweeping herbaceous undergrowth at night in high hammock with some pine and palmetto mixed in. This collection included eight male paratypes and 15 female specimens which are probably of this species, and three specimens of *pulicaria*. Other Florida series with one to four male paratypes were collected in a variety of habitats, several of which are described as follows: (1) low pine woods with thickets of wax myrtle, elsewhere a dense ground cover of palmettos, dwarf oaks and vines; (2) open grove of oaks, holly and pine on river bank, undergrowth of tree seedlings and herbage; (3) small shrubs and herbage along margin of ravine forest, and partly cleared area; (4) in shrubbery and herbage along road in open sweet gum-magnolia-oak hammock; (5) hammock bordering Newnans Lake; (6) open stand of turkey oaks on white sandy soil, with undergrowth of oak seedlings, herbs and clumped grasses, *A. litarena* mostly on herbage; (7) Lizard's tail (*Saururus*) patches in depressions in woods; (8) mesophytic upland forest; (9) salt marsh, northwest side of Cedar Key.

NOTES ON SONG.—Some notes on the song of *A. litarena* were taken on June 8, 1931, on the shore of Harkers Island, Carteret County, N. C., where all the males collected were of this species. At a temperature of 72°F. at night, the song was a series of short trills varying from 9 to 16 per 10-second period, the trills being longer than the rests and of variable length. The rests were very brief so that the song of a group appeared to be continuous. The singing started in late afternoon and continued all night and part of the morning. The crickets were silent after about 10 a.m. At a temperature of 85°F. in the morning, one was counted doing 24 trills in 10 seconds and another at a slower rate of 16 per 10 seconds. The sound was high-pitched but not as clear as that of some crickets. It was very similar to the song of *A. delicatula* of inland marshes.

Four males of *Anaxipha litarena* were collected on a sand ridge near Carolina Beach, N. C., on April 20, 1930. One was kept alive in a jar for observation on the song. At 67°F. the next night, the song was similar to that observed on Harkers Island, a series of shrill trills, about 8 per 10 seconds and each trill of about one second's duration. On April 30, at 75°F. the same cricket sang with 13 to 20 trills per 10 seconds. A caged cricket of the same species from Newnans Lake near Gainesville, Fla., supplied by T. H. Hubbell, sang in a very similar manner. The trills were of variable length and sometimes were in series of three or four separated by somewhat longer pauses. At Carolina Beach, N. C., at about 70°F. on the night of June 12, 1930, a song was heard in *Iva* bushes on the first dune, with 20 to 24 trills per 10 seconds. Three specimens which were caught proved to be *A. litarena*. One of these was later selected as the type, and the other two as paratypes.

SUMMARY

Prior to 1912 only one species of *Anaxipha* was known to inhabit the United States. This species, *A. exigua*, is widely distributed over the eastern half of the

nation. From 1912 to 1916, four more species were recognized in the United States and in 1924 the names of two species were changed. Since 1924 most students of the Orthoptera have followed Hebard in recognizing five species, namely, *imitator*, *exigua*, *scia*, *pulicaria* and *delicatula*. In the present work, the writer has found new diagnostic characters in the concealed male phallus, and, for certain species, in the ovipositor, tarsal claws and hind tibial spines. The most unique phallus was found in *A. imitator*. A very distinct type of phallus was also found in a new species, *A. litarena*, which is apparently related to *delicatula*. No characters were found for separating the two species in the female sex. A key for identification of the six species is included.

The stridulation and most-frequented habitats are described by the writer from his own notes or those of other collectors or from the literature. *Anaxipha exigua* in North Carolina has three types of song, which have not been correlated with any specific characters. One type is found most frequently in shady marshes. The other two are associated with thickets in sunny uplands, both being found in the same habitats.

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THE PHYLOGENETIC MIGRATIONS OF THE AMBIENS MUSCLE

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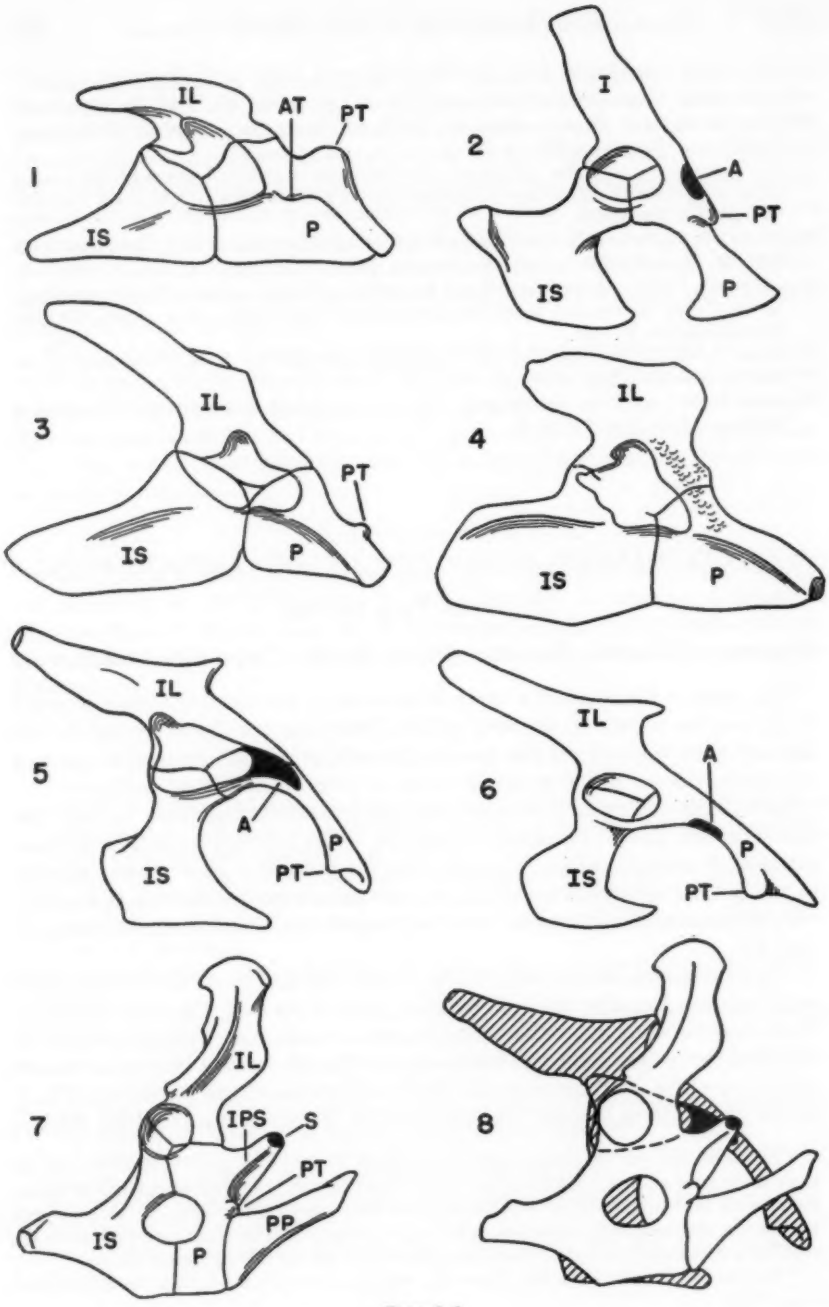
This paper is the result of a study undertaken to determine the place of origin of the ambiens muscle on the bony pelvis of early theropsid[1] reptiles and to help determine the homology of this muscle. Out of this work there has also grown a new interpretation of the prepubic bones of lower mammals.

THE LATERAL PUBIC TUBERCLE AND THE PELVIC ATTACHMENT OF THE AMBIENS IN THE EARLY THEROPSID REPTILES.—The ambiens[2] muscle is a crural extensor. It takes its origin in lizards from the pubis at a place shortly anterior to and usually somewhat ventral to the acetabulum and is inserted, in common with the femorotibialis muscle, into the preaxial side of the proximal portion of the tibia.

The ambiens has been thought to have been attached to the prominent lateral pubic tubercle found on the bony pelvis in some of the early theropsid reptiles of Permocarboniferous times. This tubercle occurs in the order Pelycosauria among the primitive pelycosaurs, the ophiacodonts (Fig. 3), but not in more advanced pelycosaurs (Fig. 4). It occurs also in the somewhat lizard-like *Araeoscelis* (Fig. 1) of the Texas Lower Permian. In these reptiles the dorsal margin of the pubis is

[1] Following the general classification based by E. S. Goodrich and D. M. S. Watson on their theories of an early dichotomy in reptilian phylogeny, the group Reptilia Theropsida includes all the "mammal-like" reptiles in the broadest sense of the term, i.e., all those reptiles on the theropsid side of the basic split into sauropsid and theropsid reptiles. All living reptiles are sauropsid reptiles. Mammals arose from among the theropsid reptiles.

[2] The terminology used in this paper for reptilian musculature is that used by Romer (e.g., 1942).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Figs 1–8

typically formed into a thick, rounded ridge which passes anteriorly and ventrally from the region of the acetabulum to terminate distally on a level with the pubic symphysis. A varying distance anterior to the acetabulum, a tubercle—the lateral pubic tubercle—projects dorsally from this ridge. The tubercle varies in size; although that of *Araeoscelis* is large in side view, it is laterally compressed. Writing their monograph on the pelycosaurs, Romer and Price (1940, p. 132) thought that this tubercle marked the site of origin of the ambiens: "All well-preserved specimens show definite indications of a point of attachment for the ambiens and pubotibialis muscles. In primitive forms this takes the form of a lateral pubic tubercle projecting above the [pubic] ridge; in others this tubercle is reduced or absent and may be replaced by a heavy rugosity close to the acetabulum." This description of the attachment of the ambiens to the lateral pubic tubercle leads, as we shall see, into difficulty when considering the muscle's homology.

Writing on *Araeoscelis*, I noted a less pronounced ventral projection (Fig. 1, AT) from that part of the pubic ridge between lateral pubic tubercle and acetabulum (1955). There seems to have been an emphasis on tendinous rather than fleshy attachment of limb muscles in *Araeoscelis*, and I believe it was this emphasis that was responsible for the ventral projection. *Araeoscelis* was a reptile of lizard-like habitus but was theropsid, i.e., it seems to have been a lacertoid experiment of the early theropsid reptiles. This lacertoid habitus makes it perhaps more reasonable in *Araeoscelis* than in any other theropsid reptile to expect to be able to use comparisons with lizards in reconstructing the musculature.

In lizards the ambiens has its origin on the pubis shortly anterior to the anterior rim of and ventral to the level of the center of the acetabulum. In *Iguana* (Fig. 5) the origin lies for the most part on a level with the most ventral portion of the acetabulum, but a small slip of the head of the muscle reaches posteriorly for a short distance in attachment to the anteroventral part of the articular capsule. In *Basiliscus* (Fig. 6) the origin lies entirely ventral to the acetabulum. Among other living reptiles, the origin lies entirely ventral to the acetabulum in crocodilians (Romer, 1923) and mostly below the level of the center of the acetabulum in *Sphenodon* (Fig. 2).

The lateral pubic tubercle is variable in its position. It lies ventral to the level of the acetabulum in the ophiacodontid pelycosaur *Varanosaurus* (Fig. 3). It is

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FIG. 1–8. The bony pelvic girdles of selected forms. FIG. 1. The early theropsid reptile *Araeoscelis*. × 1.3. FIG. 2. The rhynchocephalian *Sphenodon*. × 1.5. (After Gregory and Camp, 1918.) FIG. 3. The ophiacodontid pelycosaur *Varanosaurus acutirostris*. × 0.6. (After Romer and Price, 1940.) FIG. 4. The sphenacodontid pelycosaur *Dimetrodon limbatus*. × 0.25. (After Romer and Price, 1940.) FIG. 5. The lizard *Iguana iguana*. × 1.3. FIG. 6. The lizard *Basiliscus basiliscus*. × 3.7. (After Snyder, 1954.) FIG. 7. The monotreme *Ornithorhynchus*. × 1.2. (After Pearson, 1926.) FIG. 8. The pelvic girdle of *Ornithorhynchus* superimposed on the pelvic girdle of *Iguana*. Cross-hatched area, that portion of the pelvic girdle of *Iguana* not covered by the *Ornithorhynchus* bones. Broken line, outline of that portion of the acetabulum of *Iguana* that is hidden by the *Ornithorhynchus* bones. A, area of attachment of the ambiens muscle; AT, tubercle for the ambiens muscle; IL, ilium; IPS, iliopectineal spine; IS, ischium; P, pubis; PP, prepubic bone; PT, pubic tubercle; S, area of attachment of the sartorius muscle.

ventral to and far removed from the acetabulum in *Iguana* and *Basiliscus* but nearer to the acetabulum in some other lizards, e.g., *Eumeces*. It lies ventral to the level of the acetabulum in *Sphenodon* but no farther removed from it than in *Araeoscelis*. Although the tubercle of *Araeoscelis*—directed somewhat laterally as well as dorsally—lies on a level with the center of the acetabulum, its obvious similarity in topographical relationships to the tubercle of *Varanosaurus* justifies its being called the lateral pubic tubercle. Although directed dorsally, the tubercle of *Varanosaurus* is obviously the same structure as the laterally directed tubercle of *Sphenodon* and lizards. The more strongly lateral direction of the lacertilian tubercle may be due to the fact that in lizards the puboischiadic ligament, attached to the tubercle along with the inguinal (iliopubic) ligament and providing a surface of origin for powerful flexor muscles, is probably more strongly developed in these forms, whose bony pelvis is incomplete ventrally, than it had to be in Permian reptiles, which had an almost completely continuous sagittal symphysis from the anterior to near the posterior edge of the puboischiadic plate. That is, the laterally directed pull of the flexor muscles is concentrated on the anterior and posterior points of attachment of the puboischiadic ligament in lizards but was more evenly distributed along the whole length of the sagittal symphysis in Permian reptiles. More evidence, probably related to the preceding, for the homology of the theropsid and lacertilian tubercles may be drawn from the rather twisted appearance of the lacertilian pubis: The anterior part of the morphologically medial surface of the lizard's pubis is turned so as to face anteriorly (part of the puboischiofemoralis internus muscle arises from the "anterior" surface of the pubis) while this same surface in *Varanosaurus* and *Dimetrodon* is strictly a medial one; the lateral direction of the lacertilian tubercle may be looked upon as a phase of a more profound twisting of the whole pubis.

In none of the living reptiles described is the ambiens attached to the tubercle. It seems much more likely, therefore, that the ambiens of *Araeoscelis* was attached to the ventral projection from the pubic ridge rather than to the lateral pubic tubercle. This is in agreement with what Romer (1922, p. 563) had said earlier: "The origin of this muscle [the ambiens] (and the pubo-tibialis) in Permian fossils may be always recognized as a roughened area on the pubis anterior to and below the acetabulum." The "roughened area" is clearly illustrated in Romer's 1922 figure of a *Dimetrodon* pelvis. Romer, in 1922, was writing only of advanced pelycosaurs which lack the lateral pubic tubercle; the point made and stressed here is that the ambiens was probably never attached to this tubercle as it was later thought to have been.

The lateral pubic tubercle of *Araeoscelis* and primitive pelycosaurs must have served some useful purpose. The puboischiofemoralis internus muscle of these reptiles undoubtedly passed from the medial surface of the pelvis outward under the inguinal ligament and through a notch formed between the lateral pubic tubercle and that portion of the pubis immediately anterior to the acetabulum; this was probably also the passageway for the femoral nerve. The inguinal ligament of these early theropsid reptiles was probably attached, as it is in lizards, to the lateral pubic tubercle. I suggested in 1955 that the tubercle served to raise

the anteroventral anchoring place of the inguinal ligament and that the presence of the tubercle is to be correlated with the absence of a good anterior extension of the iliac blade. When the pelves of ophiacodonts (Fig. 3) are compared with those of more advanced pelycosaurs, sphenacodonts and edaphosaurs (Fig. 4 for the sphenacodontid *Dimetrodon*), the latter, almost without exception, are seen to differ from the first by the lack of a lateral pubic tubercle and by the presence of a good anterior extension of the iliac blade. This anterior extension permitted the inguinal ligament, even in the absence of a raised anteroventral anchoring point, to course above the puboischiofemoralis internus muscle and the femoral nerve without restricting their passage. The anterior extension of the iliac blade is, of course, concerned with more profound changes in the placement of dorsal limb musculature. The forward expansion of the iliac blade represents an enlargement of surface area for the origin of the gluteal musculature and is associated with more efficient posture and locomotion; it indicates the beginning of the trend away from a sprawling gait and toward the condition seen in mammals—with knees turned in under the trunk (see Gregory and Camp, 1918; Romer, 1922). Indirectly, then, these more important changes rendered the lateral pubic tubercle unnecessary.

The theropsid *Araeoscelis* had a lateral pubic tubercle not because it was primitive—*Araeoscelis* was in many ways a specialized reptile—but because its specialization was in a lacertoid direction and not toward a mammal-like organization.

PHYLOGENETIC MIGRATIONS OF THE AMBIENS.—There has been in recent years a growing uncertainty as to the homology of the ambiens muscle. This can be illustrated in no better way than by quoting the changing opinions of Romer: In 1922 (p. 563) he considered the homology of the reptilian ambiens and the mammalian sartorius "unquestionable"; in 1949 (p. 273) he thought, "The reptilian ambiens is presumably the sartorius. . . ."; in 1955 (p. 285) he said ". . . the homology of the ambiens of reptiles with the sartorius is less certain [than that of the iliotibialis and femorotibialis with, respectively, the rectus femoris and vasti of the quadriceps femoris]."; and in 1956 (p. 225) he feels that ". . . it is far from sure that the ambiens of reptiles is the same as the sartorius . . . of mammals."

Gregory and Camp (1918) adopted the view that the sartorius of mammals represents the anterior portion of the reptilian iliotibialis, and they were followed in this by Howell (1944, e.g.). Haines (1934, 1935b) would derive the sartorius from the anterior part of the puboischiotibialis (Haines' "adductor tibialis"; see discussion of terminology in Romer, 1942). Gregory and Camp, as did Haines (1934), considered the mammalian rectus femoris to be the homologue of the ambiens. As to the theory of homology between the sartorius and the anterior part of the iliotibialis: Bardeen (1906, p. 303) described the sartorius of man as developing ". . . from an anlage not directly fused with that of the quadriceps. Gräfenberg has described a fusion near the ilium of the proximal ends of the anlages of the rectus muscle and the sartorius with that of the iliacus. In those embryos I have studied in which these anlages are beginning to appear the quadriceps anlage is quite distinct from that of both the sartorius and iliacus. The

upper limit of the sartorius anlage approaches closely, however, the iliacus anlage." The sum of this is that the sartorius is more closely associated with the iliacus in development than with any other muscle. This would seem to correspond to the close association during the embryological development of the lizard (Romer, 1942) of the ambiens with the puboischiofemoralis internus, which latter muscle gave rise to the iliacus; the ambiens and the puboischiofemoralis internus are both constituents of the anterior half of the cleft dorsal muscle mass, while the iliotibialis is a constituent of the posterior half. The ambiens of the adult lizard often receives slips from the puboischiofemoralis internus (Romer, 1922). The so-called sartorius of birds is a part of the iliotibialis complex, but it was differentiated in a line of evolution widely divergent from that leading to mammals and is not the equivalent of the sartorius of the latter group (Romer, 1927). Romer (1922) thought the mammalian derivative of the anterior portion of the iliotibialis to be the rectus femoris. Haines' reasons for supposing the rectus femoris to be the homologue of the ambiens were: (1) He could not accept Romer's view of 1922 that all the glutei—including the gluteus maximus—were derived from the reptilian iliofemoralis which reaches only half-way down the femur. (2) He felt that the only muscle which could have given rise to the gluteus maximus was the iliotibialis. (3) He thought it unlikely that the iliotibialis could have given rise to the rectus femoris as well. (4) This left only the ambiens to become the rectus femoris. Romer (1955, e.g.) has recognized the justice of Haines' objection to the derivation of all the glutei from the iliofemoralis and has suggested that the iliofibularis may have given rise to the gluteus maximus, but other authors (e.g., Appleton, 1928) consider the mammalian tenuissimus to be the equivalent of the iliofibularis. I cannot see why it should be so unlikely that the part of the iliotibialis innervated by the femoral nerve gave rise to the rectus femoris, leaving the part with sacral innervation to become gluteus maximus. A stronger objection to Haines' theory arises from the corollary to which it led him, viz., that the sartorius arose from the anterior part of the puboischiotibialis. If the rectus were derived from the ambiens, Haines felt, only the anterior part of the puboischiotibialis in the reptile and the sartorius in the mammal would be left unaccounted for; Haines considered the two to be homologous. But this would involve the derivation of a muscle, the sartorius, innervated by the femoral nerve from an obturator-innervated one. To this, Haines had no objection; he has protested against absolute reliance on the theory of constancy of muscular nerve supply (1934, 1935b). But, even though he may be justified in this protest, we ought first to exhaust all other theories of homology for a muscle before we allow it an evolutionary shift in its innervation. Haines' argument was partly based on his supposition that the crocodilian ambiens part 1, supplied by the femoral nerve, was the homologue of the anterior part of the lacertilian puboischiotibialis, but Romer (1942) has answered that the crocodilian element is a dorsal muscle which appears to be a subdivision of the ambiens. Bardeen's observation of the close relationship of the anlagen of the sartorius and iliacus can be used too as counterargument against Haines' view. Besides this, there is the following suggested history which supports Romer's ideas on the ontogenetic and phylogenetic migrations of the ambiens.

Romer (1922, p. 563): "In the monotremes, the homologue of the sartorius of higher mammals arises from [an area on the pubis anterior to and below the acetabulum] . . . , and hence the homology of the two muscles [ambiens and sartorius] seems unquestionable. In the higher mammals it originates from the anterior superior spine of the ilium and is not closely associated with the quadriceps. This change of position may be easily accounted for by the assumption that, with the changed position of the leg, it has migrated upward over Poupart's [the inguinal] ligament, which here inserts close to the origin of the muscle; it is on the ligament in some marsupials." If Romer's theory is correct, there is one portion of the ambien's route which needs elucidation: the passage of the muscle from its position anteroventral to the acetabulum to a position on the inguinal ligament. This passage must be reconciled with non-attachment of the ambiens to the lateral pubic tubercle—the ventral attachment of the inguinal ligament—in early theropsid reptiles. Except in *Araeoscelis* which was far from the line of evolution to mammals, movement of the ambiens to the region of the pubic tubercle prior to migration on to and up the inguinal ligament would have meant a movement ventrally preceding a movement dorsally; this would conflict with what seems to have been primarily a horizontally forward movement.

Two processes of the *Ornithorhynchus* pelvis are important here. One is the iliopectineal spine (Fig. 7, IPS): Although this structure is greatly enlarged as compared with the iliopectineal "eminence" of therian mammals, e.g., that of *Didelphys* (Fig. 9, IPE), and although the spine of *Ornithorhynchus* is a process of the pubis alone while the eminence is formed by both pubis and ilium, the spine and the eminence are undoubtedly basically equivalent. This is evident both from their general similarity in topographical relationships and from the fact that both the spine and, in marsupials, the eminence serve as the pelvic point of attachment for the psoas minor muscle. The eminence does not receive the insertion of the psoas minor in all therian mammals, but the fact that it does so in marsupials (Gregory, 1947) seems significant. The other process is the pubic tubercle (Fig. 7, 9, PT): The pubic tubercle of *Ornithorhynchus* is a process of the pubis as it is in eutherian mammals. In *Didelphys* it is located on the most proximal portion of the prepubic bone and is not, strictly speaking, "pubic," but it is obviously the functional equivalent of the pubic tubercle of other forms; the tubercle as a functional process has simply moved a very short distance from pubis to prepubis in *Didelphys*. The ventral end of the inguinal ligament[3] is attached to the pubic tubercle (see Pearson, 1926, fig. 4 for *Ornithorhynchus*), and this latter structure may be considered the homologue of the lateral pubic tubercle of reptiles. The inguinal ligament of the *Didelphys* embryo (see below) is attached as much to the pubis as it is to the prepubis.

The sartorius of *Ornithorhynchus* takes origin from the apex of the iliopectineal spine (Pearson, 1926; Fig. 7, S). As Romer has indicated, this position of origin resembles that of the reptilian ambiens. This can be most clearly demonstrated

[3] For those mammals in which no true inguinal ligament exists in the sense of its being attached to the ilium as well as to the pubis, the term as used throughout this discussion refers to the free posterior edge of the external abdominal oblique muscle between which and the bony pelvis the iliopsoas muscle and the femoral nerve and vessels pass to the thigh.

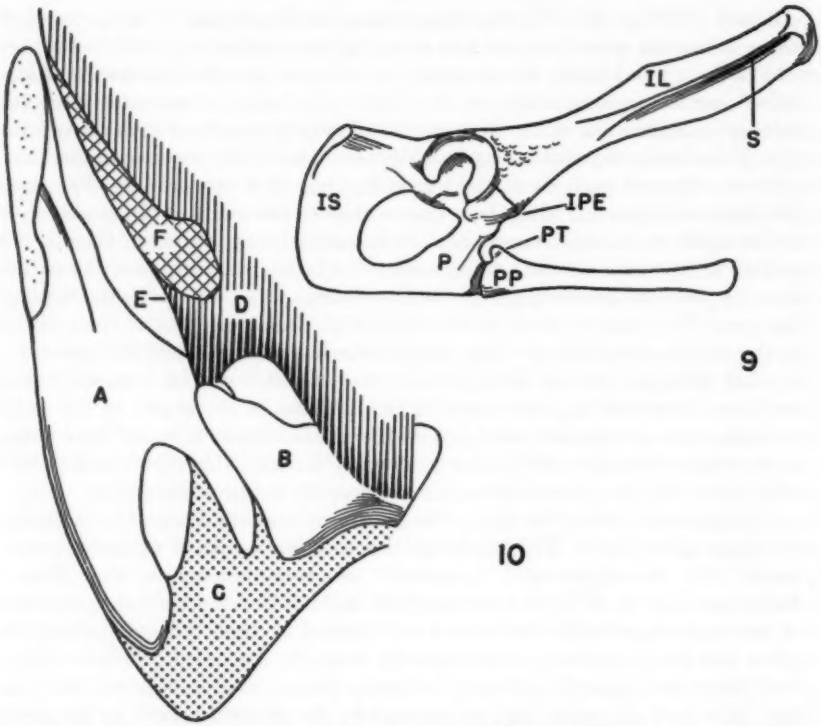

FIG. 9. The pelvic girdle of the adult opossum *Didelphys virginiana*. × 1. IL, ilium; IPE, iliopectineal eminence; IS, ischium; P, pubis; PT, "pubic" tubercle; S, area of origin of the sartorius muscle. FIG. 10. The pelvic girdle and inguinal ligament of a 10.5-mm. opossum, indicating the area of origin of the sartorius muscle. × 117. A, precartilaginous portion of the innominate bone (posterodorsal portion of ilium omitted); B, posterior portion of the precartilaginous prepubic bone; C, plate of condensed mesenchyme; D, posteroventral portion of the external abdominal oblique muscle; E, the inguinal ligament; F, the area of origin of the sartorius muscle.

by superimposing the pelvic girdle of *Ornithorhynchus* onto that of a lizard of about the same size (Fig. 8); the positions of origin relative to the centers of the respective acetabuli are then seen to be closely similar. The same effect results from superimposing the pelvis of *Ornithorhynchus* onto that of *Sphenodon*. Comparing *Araeoscelis* with *Ornithorhynchus* in the same way, the position of the ambiens tubercle may be seen to correspond closely with the position of the apex of the iliopectineal spine. The only really noticeable shift in relative position of the muscle's head from reptile to monotreme is a short forward movement which is in large part really an anterior concentration of the fibers of origin. This is perhaps to be correlated with the beginnings of a new style of locomotion, a style dependent upon the bringing of the leg under the trunk. The sartorius of higher

mammals assists in this by adducting the femur in addition to performing its old reptilian function as a crural extensor. Although the usual terrestrial gait of the platypus is "still" sprawling and rather reptile-like, the placement of the origin of its sartorius in a position more suited to adduction of the thigh than is that of the ambiens probably marks either an early stage in this trend or a vestige of progress. Putting aside the short forward movement for the moment and concentrating on the significant fact of basic retention of the reptilian position of the muscle, why is it that the sartorius of monotremes takes origin on a spine projecting anteriorly from the main body of the innominate bone?

When, by using some such tool as comparison by means of Cartesian coördinates, the pelvis of an early theropsid reptile is compared with that of a theropsid reptile well advanced toward a mammalian organization, e.g., the therapsid *Cynognathus*, and when the pelvis of this therapsid reptile is in turn compared with that of a primitive mammal such as *Didelphys*, we see in the series early theropsid-therapsid-mammal, besides the more obvious anteriorly directed shifting of the iliac blade, a progressive, posteroventrally directed buckling of that region of the pelvis shortly anterior to the acetabulum over which the puboischiofemoralis internus muscle or its homologue the mammalian iliopsoas passes on its way to the femur. This is correlated with a general backward shifting of the pubis and ischium. Gregory and Camp (1918) have explained these changes: The posteriorly directed shift of the pubis and ischium and the anteriorly directed shift of the ilium made possible the locomotory advantage of more directly backward and forward action on the femur of the adductor and obturator and the gluteal muscles; the posteroventrally directed buckling of the region of the pelvis just anterior to the acetabulum was associated with the movement of the puboischiofemoralis internus away from its reptilian place of origin on the medial surface of the pelvis and upward to its attachment as the iliopsoas to the ilium and lumbar vertebrae. It was this buckling of the anterior part of the pelvis which, so to speak, left the ambiens-sartorius stranded on either a bony anterior projection of the innominate bone as in *Ornithorhynchus* or, as we shall see, a ligament passing anteriorly from the iliopectineal eminence. It is interesting here that the ambiens of birds, too, takes origin from an anterior process of the pelvis.

This brings us to the solution of our problem. It seems improbable that the ambiens migrated ventrally to reach the ventral attachment of the inguinal ligament, but the muscle did migrate to the ligament. The initial movement of the ambiens must have been a strictly forward one—a largely relative but also somewhat absolute shift—via either an iliopectineal spine or iliopectineal fascia directly to its new place of origin on the inguinal ligament. The pubic tubercle was bypassed.

The portion of the iliopsoas muscle of mammals anterior to the inguinal ligament is covered on its non-osseous surface by the iliac fascia which is continuous posteriorly under the ligament with the iliopectineal fascia covering the femoral portion of the muscle. In man the iliopectineal fascia forms a thickened band, the iliopectineal ligament, extending from the inguinal ligament to the iliopectineal eminence and thus separating the iliopsoas muscle and femoral nerve within the

so-formed muscular lacuna from the femoral vessels within the vascular lacuna. A bony iliopectineal spine is not peculiar to the monotremes but is found also in kangaroos, for example, where it is called simply the "pectineal process"; it is a process of the pubis in kangaroos as in *Ornithorhynchus*, but we shall regard it only as a functional projection and not be concerned with its exact homology. In the kangaroos (Gregory, 1947), as in *Ornithorhynchus* (Pearson, 1926), the psoas minor muscle is inserted on the iliopectineal spine. The psoas minor, flexing the pelvis on the trunk, is not a functionally insignificant muscle and in many lower mammals is larger than the psoas major. The iliopectineal spine probably exists primarily for the insertion of the psoas minor and secondarily for the insertion of other muscles—the sartorius in *Ornithorhynchus* and the pectineus in kangaroos. That is, the sartorius of monotremes is placed where it is because of factors discussed above, but it has a bony origin only because of the existence of a spine for the insertion of another muscle. The iliopectineal fascia covers the psoas minor, and it—or, especially, its localized thickening, the iliopectineal ligament—therefore has the same general topographical relationships as an iliopectineal spine. The forward migration of the ambiens may have taken place along the iliopectineal fascia in some lines and along an iliopectineal spine in other lines of evolution. Or, the ambiens may have followed a ligamentous route in all lines and become only secondarily attached to a newly-formed process for the psoas minor in certain groups. Considering the negative evidence of the fossil record, it would certainly be hazardous to theorize a migration along a spine in all lines followed by disappearance of the spine in some. This paper makes no suggestions as to the phylogenetic positions of monotremes and marsupials within the Mammalia.

It is difficult to decide on the place of origin of the ambiens of therapsid reptiles. It is improbable that it still arose anteroventral to the acetabulum as it did in the early theropsids, and the iliopectineal eminence was not strongly developed. Presumably, it arose from either the iliopectineal fascia or the inguinal ligament. The head of the ambiens may possibly have already lain directly anterior to the acetabulum although still on the bony pelvis in advanced pelycosaurs, on, as Romer and Price (1940) supposed, a heavy rugosity close to the acetabulum (Fig. 4).

The forward and upward movement of the puboischiofemoralis internus to become the iliopsoas may have helped clear the route of the forwardly migrating ambiens.

There are many variations among mammals in the origin of the sartorius of which some may represent arrested stages in the primary, forward migration of the ambiens while others may represent the utilization of the same route in secondary return. For examples, the sartorius arises from the iliopectineal eminence in *Orycteropus*, from the immediate neighborhood of the eminence in *Tupaia*, from both the eminence and the tendon of the psoas minor in *Erinaceus*, from the fascia of the iliopsoas in *Chlamyphorus*, from the tendon of the psoas minor in *Dasypus* and from the inguinal ligament in *Sciurus* and many others (Leche, 1887; Bardeen, 1906; Howell, 1944; Haines, 1935b). Besides its primary origin from the anterior superior iliac spine, the sartorius of man may have acces-

sory slips from the iliopectineal line, the iliopectineal eminence or the inguinal ligament.

The movement of the ambiens to become the sartorius was a forward one, and the further evolution of the sartorius has seen a continuation of this trend. As shown above, the initial movement was to a large extent a relative one, but even this initial movement had an absolute component. Later, further modification of the build of the ilium made possible movement to a bony attachment still farther anterior. Until the ilium underwent a more extensive anteriorly directed shift, forward migration of the ambiens had its limit at the most anterior part of the inguinal ligament except in those forms which had a long iliopectineal spine; the apex of the iliopectineal spine of *Ornithorhynchus* lies somewhat anterior to the inguinal ligament (Figs. in Pearson, 1926). The shifting forward of the ilium which brought its apex into a position far anterior to the acetabulum, a condition seen in many mammals, presented, as it were, the sartorius with the opportunity to travel up the inguinal ligament and, in many cases, to become attached to the region of the anterior superior iliac spine. The attachment of the sartorius to the inguinal ligament in many eutherian mammals may be correlated with either a restriction or a secondary reversal of this iliac shift.

ONTOGENETIC MIGRATION OF THE SARTORIUS IN DIDELPHYS.—In the adult *Didelphys* (Fig. 9) the sartorius takes origin from the lateral iliac crest a short distance posterior to the apex of the ilium. Whereas the iliacus muscle in man, for example, takes origin from the internal surface of the iliac blade, this muscle in *Didelphys* arises from the area of the ilium ventral to the lateral crest. There is some question whether the external origin of the iliacus as seen in monotremes and marsupials or the internal origin as seen in higher mammals represents the primitive condition, but, either way, the area of origin of the sartorius in *Didelphys* obviously represents the anterior superior spine on the ventral edge of the ilium of other mammals.

The situation in the *Didelphys* embryo is quite different. Encouraged by the success of Cheng (1955), who was able, through his studies on opossum embryos, to follow the "reptilian supracoracoideus" in its migration upward over the scapula and in its subsequent division into the supraspinatus and infraspinatus muscles, I decided to see if it might be possible to observe the sartorius of an opossum midway in its migration up the inguinal ligament. Serial transverse sections of 7.5 mm. (Harvard series *924*), 10.5 mm. (Harvard series *614*), 13.0 mm. (Harvard series *921*) and 13.5 mm. (Wistar Institute series *17173*) *Didelphys virginiana* embryos were studied. The reconstruction (Fig. 10) of the pelvis, inguinal ligament and origin of the sartorius of the 10.5-mm. (early 13th day) opossum is presented here. This reconstruction was prepared by drawing each 12-micron section at a magnification of 175× with the aid of a camera lucida and then translating these drawings into a lateral view. The sections contained no artificial guide for their accurate orientation one with another, so the top of the gut was used as a rough guide, and an attempt was made to compensate for the curvature of the gut by referring to its known curvature as figured by McCrady (1938). It was not necessary to reconstruct the anterior portion of the prepubis,

and the lack of an artificial orientation marker would have made any reconstruction of that portion of the ilium posterior to the center of the acetabulum unreliable.

The pelvis of the 10.5-mm. opossum is constructed partly of precartilage and partly of condensed mesenchyme. The acetabular region, the ilium, the body and iliac ramus of the pubis, the body of the ischium, and the prepubis are present as a continuous body of precartilage. Despite the continuity of the pubis and prepubis at this stage, differential concentration of precartilaginous materials made it possible to observe that the lateral surface of the presumptive pubis is recessed to receive the prepubis. In each lateral half of the pelvis there is a plate of condensed mesenchyme (Fig. 10, C) connecting the precartilaginous portions of the ischium and pubis but leaving a foramen through which passes the obturator nerve. This plate of condensed mesenchyme is continued anteriorly to form a thin, laminate, ventromedially directed extension of the prepubis. The mesenchymal ventromedial extensions of the two prepubes meet in the midline. The inguinal ligament (Fig. 10, E), here defined and described as that portion of the free posterior edge of the external abdominal oblique muscle running upward from the attachment of the muscle to the "pubic tubercle," is attached as much to the presumptive pubis as it is to the prepubis. This attachment can be easily made out at a knee between the body and the iliac ramus of the pubis. Any attachment of the inguinal ligament to the iliac blade could not be clearly made out, but the ligament and the blade can be seen to approximate one another as the two are traced posterodorsally. There is a gap, the subcutaneous inguinal ring, between the attachment of the external oblique to the "pubic tubercle" and its more anterior, purely prepubic attachment. (See below under section on prepubis for further remarks on the pelvic girdle of the *Didelphys* embryo.)

Except for loose mesenchymal connections, the head of the sartorius of the 10.5-mm. *Didelphys* is not actually fastened to the inguinal ligament—or to any other structure—but it is separated from the ligament by a space of only 30–40 micra and thus may be said, for our purposes, to take origin from it. The origin of the sartorius (Fig. 10, F) is not confined to the very edge of the external abdominal oblique but occupies a narrow band on the external surface of the muscle immediately adjacent to and including its free posterior edge. This band of origin begins some distance posterodorsal to the "pubic tubercle," extends posterodorsally in the same direction as does the inguinal ligament, and tapers to a point well before the apex of the ilium is reached. The bulk of the fibers take origin from that part of the band directly anterior to a gentle swelling on the front rim of the acetabulum which may possibly represent the adult iliopectineal eminence; the embryonic iliopsoas passes outward under the ligament over, anteroventral to, and posterodorsal to this swelling, but it was not possible to detect any genuine attachment of fibers here to mark out a psoas minor. The early stage of differentiation would, of course, make it unreasonable to expect to be able to identify the future iliopectineal fascia. The most distal portion of the sartorius was difficult to define in the 10.5-mm. embryo but was easily followed to the tibia in a 13.5-mm. specimen. The nerve to the sartorius enters the deep surface of the muscle; it was traced to its parent trunk, the femoral nerve, by graphic recon-

struction. There is no question as to the identification of the sartorius: Its superficial position distinguishes it while the rectus femoris, the only muscle with which it might have been confused, was found lying more deeply and ventrally and supplied by a more distal trunk of the femoral nerve in common with the underlying vasti.

Two features deserve attention here: the obvious fact of attachment of the sartorius to the inguinal ligament, and the fact that the sartorius is in its position on the inguinal ligament before the ilium is extended anteriorly. Both these features would seem to correspond with an earlier stage of mammalian organization.

It would seem, then, that Romer was correct in 1922 when he considered the homology of the ambiens with the sartorius to be certain and when he assumed that the muscle migrated upward over the inguinal ligament to the anterior superior iliac spine.

POSSIBLE OTHER FUNCTIONS OF THE LATERAL PUBIC TUBERCLE.—The lateral pubic tubercle of early theropsid reptiles was the site of ventral attachment of the inguinal ligament. It very probably did not, as Romer and Price suggested, support the head of the ambiens, but these authors thought that the tubercle was the proximal site of attachment of the pubotibialis muscle too.

The pubotibialis in lizards is an obturator-innervated crural flexor arising from the pubis and inserting on the fibular aspect of the proximal end of the tibia. Its area of origin is anteroventral to that of the ambiens, usually extends ventrally to reach the lateral pubic tubercle, and is at least near the tubercle; it arises wholly from the lateral pubic tubercle in at least the 9-mm. embryo of *Lacerta muralis* (Romer, 1942). Possibly, a pubotibialis was attached to the lateral pubic tubercle in early theropsid reptiles. Romer felt in 1922 that the pubotibialis was lost during the evolution to mammals and still (1955) considers its fate a moot question; Haines (1954) thought it to be present in mammals as the adductor longus.

Some work of mine indicates that the pubotibialis may possibly be present in mammals as a constituent of the pectineus. The pectineus, usually a short femoral adductor originating on the pubis, is found in two more or less distinct portions in many mammals including man—where there is great variation in the degree of separation. In some mammals both parts are innervated by the femoral nerve, in others both parts are innervated by the obturator nerve, and in still others one part is innervated by the femoral nerve and the other by the obturator nerve (Bardeen, 1906). In man the usual innervation is femoral, but there may be an additional supply from the obturator or the accessory obturator nerve; when both femoral and obturator supplies are present, the femoral nerve supplies a superficial lamina while the obturator nerve is distributed to a deeper lamina.

In the adult *Didelphys virginiana*, the pectineus takes a restricted origin from the "pubic" (really prepubic, but see below) tubercle, spreads, splits and inserts into the pectineal line of the femur as a proximal part and a more distal part separated by a blood vessel. The femoral nerve innervates both parts while the obturator helps supply the more distally inserted part.

The pectineus is divided into a dorsal and a ventral lamina in the 13.5-mm.

Didelphys embryo. The two laminae are united along their anterior borders but diverge posteriorly where a blood vessel comes to lie between them. Two branches of the femoral nerve unite and plunge downward into the dorsal lamina to join a branch of the obturator nerve which passes upward through the ventral lamina. At the proximal end of their united anterior borders both laminae are attached to the area of the "pubic tubercle." The dorsal lamina can be traced posteriorly and under the inguinal ligament to where it merges with the mass of the embryonic iliopsoas muscle.

Gregory and Camp (1918) and Romer (1922 and later) considered the pectineus to be derived as a minor element along with the iliopsoas as the major element from the reptilian puboischiofemoralis internus. With this I would agree—in part. The dorsal lamina of the embryonic pectineus of *Didelphys* is clearly associated with the iliopsoas. But I believe that the ventral, obturator-innervated lamina may represent the reptilian pubotibialis.

The origin of the pubotibialis corresponds with the origin of the ventral lamina of the embryonic pectineus; both arise from the pubic tubercle. The pectineus arises from the prepubis alone in the adult *Didelphys* but from the junction of the still continuous pubis and prepubis in the embryo. The pubotibialis is inserted on the shank while the pectineus is inserted on the femur, but this is no barrier to a theory of homology: The femorococcygeus of mammals inserts in some cases on the patella, in some on both patella and femur, and in some on the femur alone (Appleton, 1928); apparently a tendon of insertion can migrate across the ligaments of the knee joint.

My studies on the *Didelphys* embryo agree fairly closely with those of Bardeen (1906) on the human embryo. Bardeen found in the 14-mm. human embryo an anlage of the pectineus, pierced by a branch of the femoral nerve, which was closely associated with another anlage which in turn was associated with the anlage of the obturator externus. Bardeen was, however, unable to trace any branch of the obturator nerve into the second anlage. Bardeen was also unable to find any fusion between the embryonic pectineus and iliopsoas; this, however, Gräfenberg (1904) observed. Bardeen (p. 303) came to the conclusion that "The dorsal or femoral portion [of the pectineus] is probably derived from an anlage intimately associated with the iliopsoas anlage, the ventral portion from the anlage of the obturator externus." My conclusion differs in that I would equate the ventral portion with a complete muscle, the pubotibialis, rather than with a part of the obturator externus.

If there be such a thing as constancy of muscular nerve supply, the facts that in some mammals the pectineus is supplied by the femoral nerve exclusively and that in others it is supplied only occasionally by the obturator nerve in addition to the femoral nerve would necessitate a belief in the possibility of transfer of nerve fibers from one trunk to another. The occasional presence of an accessory obturator nerve—really more closely associated with the femoral nerve—is a clue. Bardeen (1906, p. 303): "Nerve elements belonging to the ventral territory may be normally bound up in the femoral nerve in those branches which supply the pectineus muscle. When these branches become isolated we have the accessory obturator nerve."

The theory of homology suggested here agrees with a more general theory advocated by Howell (1938): In the evolution from reptiles to mammals there was a cleavage of both the primitive dorsal and the primitive ventral sheet of limb musculature into anterior and posterior parts. Thus the dorsal sheet with both femoral and peroneal innervation gave rise to a femoral part and a peroneal part, while the ventral sheet with both obturator and tibial innervation gave rise to an obturator and a tibial part. Howell (p. 198) noted a later ". . . trend in more advanced mammals toward the fusion of certain muscle units of dissimilar relationships, thus simulating to some extent the primitive tetrapod condition. In other words, there has been a change, from dual innervations by pairs of related nerves, to single innervations, and then a trend toward dual innervations by pairs of unrelated nerves, following fusion of unrelated muscle units . . . ." Thus, in the present example, it is suggested that the pectineus arose by a combination of a part of the femoral-innervated portion of the primitive dorsal sheet with a part of the obturator-innervated portion of the primitive ventral sheet.

THE PREPUBIC BONES OF MONOTREMES AND MARSUPIALS.—Further consideration of the buckling and shifts involved in the transformation of the reptilian into the mammalian pelvis leads to a new interpretation of the prepubic bones of monotremes and marsupials.

I submit that the prepubic bones may be analogous and perhaps even homologous with an anterior portion of the infraäcetabular part of the pubis of early theropsid reptiles. I suggest further that the prepubis represents the retention (or formation) of an anterior bony surface during the process of general displacement posteriorly of the pubis during the evolution of mammals from reptiles.

The retained bony surface probably represents a part of that portion of the reptilian pubis that lies anterior to the lateral pubic tubercle. The lateral pubic tubercle of *Sphenodon* and lizards and, as we have seen, probably of the early theropsid reptiles too, marks the site of ventral attachment of the inguinal ligament. The pubic tubercle of mammals serves the same function and generally forms the most anterior projection of the ventral part of the pubis. (The tubercle in cases like that of *Didelphys* is technically prepubic but practically pubic.) Whereas, then, a portion of the pubis lies anterior to the attachment of the inguinal ligament in *Sphenodon*, lizards and early theropsid reptiles, there is in the region immediately anterior to this attachment in mammals either no bone or the prepubic bone.

Certainly, the general appearance and location of the prepubis seem to offer evidence of this retention. This is obvious in the drawing (Fig. 8) of the superimposed pelves of *Ornithorhynchus* and *Iguana* and is perhaps even more obvious in comparing *Ornithorhynchus* with *Sphenodon* or, especially, with an early theropsid reptile such as *Araeoscelis*, the pubes of these reptiles being more expanded in an anteroposterior direction than is that of *Iguana*. No suggestions are made here as to the phylogenetic positions of the monotremes and the marsupials relative to one another, to therapsid reptiles or to the eutherian mammals, but I do believe that I am justified in regarding these primitive mammals as illustrative in many ways of an early stage of mammalian organization; they may be profitably compared with the therapsids. It is difficult to compare the pelvic

girdle of a monotreme or any marsupial having well developed prepubes with that of a therapsid reptile such as *Cynognathus* without, so to speak, seeing the prepubes in the therapsid too. Although omitting them from his later illustrations of therapsid reptiles, Romer restored in outline prepubic bones for *Cynognathus* and *Moschops* in 1922. Goodrich (1930) thought that the Cynodontia had cartilaginous prepubes. Howell (1944, fig. 21) assumed them to have been present in *Cynognathus* and, so it would seem from an inspection of his illustration, coossified with the pubes. Gregory and Camp restored prepubes for *Cynognathus* in 1918, and Gregory has since (1947, p. 37) said: "In *Cynognathus*, Seeley's (1895) specimen . . . shows a flat articular facet on the anterior transverse border of the symphysis [pubis], which suggests that the cynodonts . . . had epipubic bones." Comparing the pelves of therapsids such as *Cynognathus* and *Moschops* with the pelves of earlier theropsid reptiles such as *Dimetrodon* and *Varanosaurus*, those of the former appear to have had an anterior portion of the ventral part of their pubes boldly chopped off; any prepubis present would have occupied the space left by the missing piece of pubis. The displacement posteriorly of the major portion of the pubis was not complete in these therapsids, and any prepubis present would have been shorter than the well developed bone seen in monotremes and marsupials. If one juxtaposes a ventral view of a monotreme pelvic girdle with one of the pelvic girdle of an early theropsid reptile, a striking similarity in position between the prepubis of the one and the pubic ridge of the other becomes immediately apparent, and it is indeed difficult to avoid mentally filling in the gap between the prepubes with a plate of bone to complete what then obviously resembles the puboischiadic plate of the reptile. As to comparisons of marsupials with eutherians, it is probably true, as Romer (1945) feels, that marsupial and placental mammals have descended directly but independently from a mammalian stock geologically far older than either, but I do not feel that the presence of prepubic bones in the marsupials can be safely used as strong evidence in support of this remoteness of relationship. The prepubes of *Thylacinus* are only small, unossified fibrocartilages.

The prepubic bones are developed in the embryo ". . . from cartilaginous processes of the pubes which later become separated . . . ." (Goodrich, 1930, p. 200). In the 10.5-mm. embryo of *Didelphys* (Fig. 10) the precartilaginous prepubis is still connected with the precartilaginous innominate "bone." The inguinal ligament is attached as much to the presumptive pubis as it is to the prepubis. There is a decidedly reptilian appearance about the whole pelvis of the embryonic *Didelphys*. The presumptive ilium is directed upward and somewhat backward, and the sciatic nerve thus passes behind and somewhat below it. Looking at the prepubis of this stage as a direct, anterior extension of the presumptive pubis, the position of the ventral attachment of the inguinal ligament is seen to resemble very much the position of the lateral pubic tubercle of the early theropsid reptiles, and anterior to this the prepubis itself—relatively more robust in the embryo than in the adult—resembles the pubic ridge of the theropsids. The effect is completed by the plate of condensed mesenchyme, resembling the anterior part of the ventral portion of the theropsid puboischiadic plate, which unites the two

lateral halves of the girdle in the prepubic region. Thus the ontogenetic picture heightens the resemblance of the prepubis to the portion of the theropsid puboischiadic plate anterior to the lateral pubic tubercle.

Although Romer (1947) suggests that the fossil evidence may not be adequate, it is perhaps significant for the present discussion that most of the labyrinthodont amphibians whose pectoral girdles are known had a single endochondral element, the scapulocoracoid, in place of the scapula and coracoid found in *Seymouria* and the scapula and one or two coracoids found in their descendants the reptiles. It should not seem impossible, then, that the pubis of early theropsid reptiles gave rise to both the pubis and the prepubis of monotremes and marsupials.

In the absence of more and better evidence for a secure argument for homology, let us consider the prepubis for the moment as at least a functional representative of an anterior part of the reptilian pubis. What was the advantage to the earliest mammals of such a retention or formation?

The prepubic bones of monotremes and marsupials receive insertions of hypaxial trunk muscles and are sometimes described as sesamoid bones in one or other of these, but these muscles require no special bony process in the eutherian mammals. It is the attachment of a limb muscle which provides us with a clue: In *Ornithorhynchus* the gracilis takes origin not only from the entire length of the puboischiadic symphysis but also from the outer surface of the posterior two-thirds or so of the length of the prepubic bone (Leche, 1887; Pearson, 1926). The origin of the gracilis in the monotreme *Tachyglossus* extends anteriorly onto the base of the prepubic bone (Gregory and Camp, 1918). There seems to be general agreement (e.g., Gregory and Camp, 1918; Romer, 1922) that the gracilis is the homologue of the reptilian puboischiotibialis. In lizards this muscle arises from almost the entire length of the puboischiadic ligament; in *Sphenodon* (Gregory and Camp, 1918) it arises from the puboischiadic ligament and from the entire length of the puboischiadic symphysis. It probably arose from the entire length of the puboischiadic symphysis in the early theropsid reptiles. This extensive origin is to be correlated with the gaits of these animals. *Sphenodon* and lizards are sprawling-gaited; those lizards that are capable of bipedalism are sprawling-gaited even when running at speed (Snyder, 1949). The puboischiotibialis is primarily a crural flexor and is also able to assist in adduction and, to some extent, protraction of the thigh (Snyder, 1954). It is able to act effectively from an anteroposteriorly extensive head in forms like lizards where the hindlimb meets the trunk at a wide angle. In these animals the trunk is held above the ground almost entirely by means of muscular action—there is no ball and socket hip joint as in mammals—and the puboischiotibialis through its action as crural flexor and femoral adductor thus serves an important postural function. The wide angle of the trunk-thigh junction also makes far anteriorly placed fibers of origin effective in the action of the muscle as a femoral protractor.

We see, then, that the primitive area of origin of the puboischiotibialis-gracilis was quite extensive in an anteroposterior line. This extensive origin seems to have been retained in *Ornithorhynchus* and, to a lesser degree, in *Tachyglossus*. In the eutherian mammals there is no prepubic bone, and in some, e.g., the cat,

the gracilis does not even utilize the entire puboischiadic symphysis but takes origin from only the posterior three-fourths or so of the symphysis. But this is only to be expected: In those mammals whose knees are fully turned in under the trunk, any fibers of the gracilis from an anterior area of origin would be less effective than fibers arising more caudally, and besides, the gracilis of higher mammals generally has added a new function, drawing of the leg caudally, to its retained function of femoral adduction, thus making a concentration on posterior origin even more advantageous. Certainly, any gracilis fibers from a prepubic bone would be at a definite disadvantage in advanced mammals. We may therefore expect to see a general retreat posteriorly of the anterior edge of the gracilis as we ascend the scale of mammalian organization. Monotreme limbs and limb girdles are always described as reptile-like; Howell (1944, p. 26) considers the monotremes as "... having the typical reptilian type of limb suspension. ..." An anteroposteriorly extensive origin of the gracilis thus seems to be in its proper place in *Ornithorhynchus*. *Tachyglossus* is somewhat more advanced in this respect. In *Didelphys* the gracilis arises from only the puboischiadic symphysis but from the symphysis' whole length; only in *Myrmecobius* and *Phascolarctos* among marsupials does the gracilis have any origin at all from the prepubis (Leche, 1887). There are cases among the eutherians of a partial origin of the gracilis from the linea alba (*ibid.*); this may represent a secondary shift. The gracilis in most eutherians is restricted to the pubis and ischium or, as in man, to the pubis alone. It is interesting that in crocodilians the origin of the puboischiotibialis is confined to the ischium (Romer, 1923). This is perhaps to be correlated with the fact that their "Fast locomotion ... is accomplished with the body high off the ground and the limbs straight under the body. ..." (Romer 1945, p. 219) and the probable derivation of the crocodilians from bipedal thecodonts (*ibid.*).

I submit, then, as a possibility, that the prepubic bones represent a retention or replacement of a portion of the reptilian puboischiadic plate anterior to the lateral pubic tubercle, that this retention or replacement took place during the general posteriorward displacement of the pubis, and that at least one of the factors responsible for the presence of the prepubic bones in lower mammals was the advantage to their more or less sprawling-gaited ancestors of an anteroposteriorly extensive surface of origin for the gracilis muscle. The retention of the prepubis by marsupials, in which it no longer functions as a surface of origin for the gracilis, may be due to the bone's having been early put to secondary uses—perhaps support of the marsupium, perhaps in some way in connection with the actions of the trunk and pyramidalis muscles.

SUMMARY

The lateral pubic tubercle of early theropsid reptiles is homologous with the lateral pubic tubercle of *Sphenodon* and lizards and with the mammalian pubic tubercle—except where the mammalian tubercle is functionally replaced by a process of the prepubic bone, in which case there still exists analogy.

Although the pubotibialis muscle may have been attached to it, the lateral

pubic tubercle of early theropsid reptiles was not the site of origin of the ambiens muscle. Instead, the tubercle probably served, in the absence of a good anterior extension of the iliac blade, to elevate the inguinal (iliopubic) ligament above the course of the puboischiofemoralis internus muscle and femoral nerve. The ambiens muscle of early theropsid reptiles took its origin at a place on the pubis anteroventral to the acetabulum. With the evolution of the theropsids toward a mammalian organization, the head of the ambiens moved anteriorly: First, it moved to an area anterior to the acetabulum but still on the innominate bone. Following this, it moved farther anteriorly via either an iliopectineal spine or an iliopectineal fascia, i.e., bypassing the pubic tubercle, to become attached to the inguinal ligament. This movement anteriorly was a largely relative one, brought about by a retention by the ambiens of its position relative to the acetabulum while the pubis underwent a posteriorly directed buckling. With extensive shifting anteriorly of the ilium, the sartorius (now more firmly established by a study of its embryological history as the mammalian homologue of the ambiens) later migrated up the inguinal ligament to the anterior superior iliac spine.

The obturator-innervated portion of the mammalian pectineus muscle may be the homologue of the reptilian pubotibialis.

The prepubic bones of monotremes and marsupials may represent a remnant—or functional replacement—of a part of that portion of the reptilian puboischiadic plate which lay anterior to the lateral pubic tubercle.

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MOLLUSKS OF THE UPPER NEUSE RIVER BASIN, NORTH CAROLINA[1]

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INTRODUCTION.—This report of a freshwater mollusk survey of the Neuse River Basin attempts to meet a need created by lack of a thorough study of Atlantic drainage fluviatile mollusks in North Carolina. Several persons had studied or collected mollusks of the state in the 19th and early 20th centuries. Isaac Lea received North Carolina shells, some of which evoked descriptions of new species, e.g. *Unio pertenuis* from E. Emmons, *U. genthii* from F. A. Genth,

[1] From a thesis partly meeting requirements for the Ph.D. degree at Duke University, 1954.

and *U. conspicuus* from C. M. Wheatley (Lea, 1867, 1857, 1872 respectively). *Melania dislocata* (Ravenel, 1834) was described from Dan River, N. C. Other state records are those of Wright, 1897; Pilsbry, 1903; Walker, 1908; van der Schalie, 1933; Pearse, 1936; Goodrich, 1942, 1950; and Rehder, 1949. Ortmann (1913, 1919) studied parts or all of various easterly draining streams from Virginia to New York. Goodrich (1939) reported the mollusks, excepting unionids, of the Ogeechee River Basin, Georgia. Except for largely unreported, sporadic collecting, chiefly by C. S. Brimley, the Neuse River Basin was unknown malacologically.

The rapid growth of population and industry in the Neuse Basin made it of first importance to record the mollusks and their distribution before dams, pollution and other signs of progress altered the fauna too greatly. Also sought were as many data on life history and environment as were consistent with completing the survey. After its molluscan fauna had been determined, the Neuse Basin could be viewed in relation to other Atlantic drainages.

The Neuse River Basin extends about 180 miles southeastward from the mid-Piedmont area north and west of Durham, through the Fall Zone to New Bern in the Coastal Plain; its greatest width is about 45 miles. The river itself is about 300 miles long. Regional geology extends the fluviatile vigor of Fall Line conditions eastward as a Fall Zone which ends a few miles above Smithfield. Roughly half the basin is below that point. The upper half consists of Piedmont and Fall Zone areas. Characteristic of it are steeper gradients, riffles alternating with quieter stretches and pools, rocky, gravel and sand bottoms, and many small headstreams. Water levels vary widely here. In the lower Coastal Plain part, gradients are more gentle and soils more absorbent. Streams are larger and slower, have clayey, sandy or muddy bottoms and are less affected by drouth.

Drouth in the basin was severe in 1950 and 1951. For those two years the rainfall deficits of five weather stations averaged eight and twelve inches respectively. Although drouth gave access to otherwise inaccessible spots and specimens, it took a toll of mollusks. Most of the dead mollusks occurred in drouth-reduced small creeks and the partly exposed beds of larger streams in the upper basin.

MATERIALS AND METHODS.—In 1950 and 1951, 136 stations were established to sample upper parts of basin streams as well as points below. There were 125 in the upper basin (Fig. 1), 11 in the lower, scattered from the Wayne-Lenoir county line to just below New Bern.

All accessible habitats at a station were explored until no further species appeared. The most useful collecting tool was a ⅛-inch mesh scraper net which was used to depths of about five feet. In the deeper water of four impoundments a Peterson dredge was used, to little avail. Specimens were returned to the laboratory alive in labeled jars of stream water. After sorting and cleaning they were kept alive for observation or put in jars containing 70 per cent alcohol and a station number tag. Shells of dead unionids were given both an individual, and the station, number.

Recorded data included: width of stream; nature of bottom and substrate; depth of visibility, of stream, and of capture of specimens; pH; air and water temperatures; aquatic vegetation; miscellaneous notes on habitats of particular specimens, station descriptions, etc. Speed of flow was timed and classified as follows: slow, 0–½ m.p.h.; moderate, ½–1 m.p.h.; fast, over 1 m.p.h.

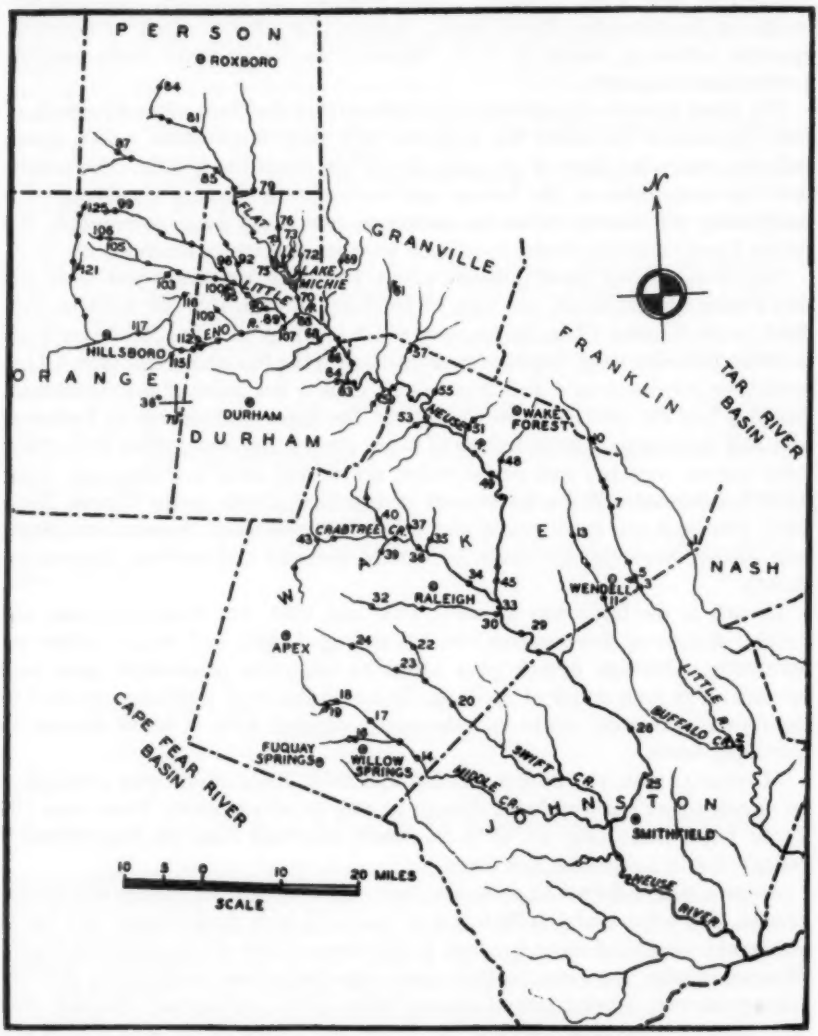

FIG. 1. Upper basin station locations. Station numbers rise as one goes upstream. Station 1 is on Moccasin Creek which joins the lower Neuse. The Little River is the next major tributary upstream, hence its stations are numbered 2–10, and so on. Station 69 is on Knap of Reed Creek. To avoid crowding station numbers, not all are shown.

Radulae were prepared by heating at least the snail's head in a concentrated solution of potassium hydroxide, washing well in water, mounting in Hoyer's medium (refractive index about 1.4) and partly disarticulating for study. Camera lucida drawings of representative radular teeth were made of *Clappia virginica*, *Mudalia carinata*, *Oxytrema catenaria dislocata*, *O. proxima*, *Ferrissia hendersoni* and *Physa inflata*. Opercula of the first four were cleaned and photographed. Specimens of *Lasmigona subviridis*, *Anodonta cataracta*, *Alasmidonta heterodon*, *Elliptio complanatus*, *Ligumia constricta* and *Lampsilis conspicua* were gravid. Glochidia were pipetted from the marsupia, washed in alcohol, stained in eosin, dehydrated, cleared, mounted in piccolyte and photographed. The various aspects of shells of all species were photographed.

Gastropod classification follows that of F. C. Baker (1928, 1945) except in the use of the generic names *Mudalia* and *Oxytrema* for *Anculosa* and *Goniobasis* respectively (Morrison, 1952, 1954). Pelecypod classification is largely that of F. C. Baker (1928). However, the subgeneric names of the genus *Anodonta* are based on data pointed out by J. P. E. Morrison (personal communication). Like *Anodonta imbecillis*, *A. cygnea*, the genotype, is monoecious (Bloomer, 1940, 1943, 1946), and has flat umbones. Therefore *A. imbecillis* is *Anodonta* s.s. For the American anodontas represented by *A. grandis* and *A. cataracta*, Crosse and Fischer (1893) created *Pyganodon*, naming *A. globosa* Lea as type species. These mussels differ from the *A. imbecillis* group in their raised umbones and in usually being dioecious.

Insofar as possible the author identified specimens by study of shell and anatomical features. These tentative identifications were confirmed or corrected by study of the U. S. National Museum collections under the guidance of Dr. J. P. E. Morrison. Dr. W. J. Clench of the Harvard University Museum of Comparative Zoology identified *Physa inflata*.

Following are the species and the total number of stations at which each occurred.

CLASS GASTROPODA

ORDER CTENOBRANCHIATA

1. *Valvata bicarinata* Lea, 1841, 1. Only dead specimens found.
2. *Campeloma decisum* (Say, 1817), 49.
3. *Amnicola* (*Amnicola*) *limosa* (Say, 1817), 2.
4. *Clappia virginica* (Walker, 1904), 11.
5. *Mudalia carinata* (Bruguière, 1792), 15.
6. *Oxytrema catenaria dislocata* (Ravenel, 1834), 22.
7. *Oxytrema proxima* (Say, 1825), 3, and an upper Cape Fear River Basin station.

ORDER PULMONATA

8. *Pseudosuccinea columella* (Say, 1817), 48.
9. *Fossaria modicella* (Say, 1825), 2.
10. *Helisoma anceps* (Menke, 1830), 47.
11. *Menetus* (*Micromenetus*) *dilatatus dilatatus* (Gould, 1841), 29.

12. *Ferrissia* (*Ferrissia*) *hendersoni* (Walker, 1908), 38.
13. *Ferrissia* (*Laevapex*) *diaphana* (Haldeman, 1841), 22.
14. *Physa inflata* Lea, 1841, 65.

CLASS PELECYPODA

ORDER PRIONODESMACEA. Family Unionidae

15. *Ligumia* (*Micromya*) *constricta* (Conrad, 1838), 9.
16. *Ligumia* (*Micromya*) *delumbis* (Conrad, 1834), 1, all dead.
17. *Lampsilis ochracea* (Say, 1817), 1.
18. *Lampsilis conspicua* (Lea, 1872), 1.
19. *Strophitus undulatus* (Say, 1817), 4.
20. *Lasmigona* (*Platynaias*) *subviridis* (Conrad, 1835), 18.
21. *Alasmidonta* (*Alasmidonta*) *undulata* (Say, 1817), 6.
22. *Alasmidonta* (*Proalasmidonta*) *heterodon* (Lea, 1830), 1.
23. *Anodonta* (*Anodonta*) *imbecillis* Say, 1829, 2.
24. *Anodonta* (*Pyganodon*) *cataracta* Say, 1817, 1.
25. *Pleurobema brimleyi* (S. H. Wright, 1897), 2.
26. *Elliptio complanatus* (Solander, 1786), 40.
27. *Elliptio complanatus roanokensis* (Lea, 1836), 6.
28. *Elliptio productus* (Conrad, 1836), 2.

ORDER TELEODESMACEA. Family Corbiculidae

29. *Polymesoda caroliniana* (Bosc, 1802), 1.

Family Sphaeriidae

30. *Sphaerium solidulum* (Prime, 1851), 35.
31. *Sphaerium striatinum* (Lamarck, 1818), 8.
32. *Musculium contractum* (Prime, 1865), 20.
33. *Musculium transversum* (Say, 1829), 3.
34. *Musculium partumeium* (Say, 1822), 3.
35. *Eupera cubensis* (Prime, 1856), 1.
36. *Pisidium dubium* (Say, 1817), 3.
37. *Pisidium compressum* Prime, 1851, 1.
38. *Pisidium peraltum* Sterki, 1900, 1.
39. *Pisidium abditum* Haldeman, 1841, 1.

Species never before reported from North Carolina by either a specific locality or an inclusive statement of range are: *Valvata bicarinata; Clappia virginica; Fossaria modicella; Musculium contractum; Pisidium peraltum.* New records for the Neuse Basin are: *Amnicola limosa; Oxytrema proxima; Helisoma anceps; Menetus dilatatus; Ferrissia hendersoni; Ferrissia diaphana; Physa inflata; Anodonta cataracta; Lampsilis ochracea; Eupera cubensis.*

The collections are divided among the U. S. National Museum, the Duke University Department of Zoology, and the author.

HABITATS. *Gastropoda.*—Environmentally and somewhat distributionally the snails fall into two groups corresponding rather well with their orders. Chief

factors considered are station location, stream flow, substrate and depths occupied.

Ctenobranchiata *Clappia virginica*, *Mudalia carinata*, *Oxytrema catenaria dislocata* and *O. proxima* compose an upper basin riffle-dwelling group of which the first two are obligate members, each with its own habitat. *Clappia virginica* was always associated with riffleweed (*Podostemum ceratophyllum*), at stations where least stream width was about 40 feet, and occurred to depths of four feet. *Mudalia carinata* was associated with algae or riffleweed. Young *M. carinata* were invariably in the upper two or three inches; adults were usually in that stratum, rarely below eight inches. Observations on the oxytremas confirm Goodrich's (1950) statement that adults may be in water of only moderate velocity, but young prefer greater velocities. In this study young oxytremas were on stones or gravel, associated with algae or riffleweed in shallow, fast currents. Habitat factors common to all four riffle-snails are moderate to fast stream flow, rocks and riffles.

Campeloma decisum occupied 49 stations. One was in a lower basin tributary, five were in the Neuse proper (all Fall Zone) and the rest were well spread through the upper basin. This snail inhabits moderate to fast waters, but not riffles, and is often shallowly buried in sandy gravel or sandy clay. If such a habitat were above or below barriers to dispersal such as riffles or dams (Bovjberg, 1952), so were the snails.

Amnicola limosa was taken at Piedmont station 58 and a lower Neuse station. The latter was the only basin locality of *Valvata bicarinata*.

Among the Pulmonata, three occurred in both upper and lower basins. It is the habit of *Pseudosuccinea columella* to move slightly out of water on the numerous projections, apparently insensitive to current as a habitat factor. *Helisoma anceps* lives in slow to moderate, rather shallow currents, on a substrate of fine particles and detritus. *Physa inflata* occurs from small creeks to large rivers in slow to moderate currents, often near or at the surface, and usually associated with plant material.

Contrasted with the three large pulmonates above are *Menetus dilatatus*, *Ferrissia hendersoni* and *F. diaphana*, small leaf-dwellers. Only the last occurred in the lower basin (one station). Their stations were in slow to moderate waters of the Neuse and tributaries, correlated with the general presence of the principal substrate, fallen leaves.

Fossaria modicella, an amphibious pulmonate (Baker, 1928) was found at two Piedmont stations (24, 54).

Pelecypoda, Unionidae. Most unionids were embedded in a sandy or muddy-sand bottom in moderate to fast upper basin currents, but *Elliptio complanatus roanokensis* was found on its side on a hard bottom in similar, Fall Zone currents. *Lampsilis conspicua* and *Anodonta cataracta* were found only in Lake Michie. The latter bivalve took the "pond-form" of Ortmann (1919); with its inflated shell, it was common on the muddy bottom. *Lampsilis conspicua*, with a heavier, less inflated shell, was found where the firm gravel-rock bottom was shallowly mud-covered.

At most of the 48 unionid-occupied stations, only one or two species were found. Six of the nine fluviatile stations which harbored more than two species were below dams. All five with four or more species were below dams (stas. 45, about a mile below Milburnie dam, 5, 6, 20, 112). Dams enrich plankton by impoundment, catch silt (see Ellis, 1931), and the falls aerate the water. Most Neuse Basin dams leaked enough to maintain at least a moderate current below, even at the height of the 1951 drouth. It seems reasonable to assume that these effects of dams make possible satisfactory minima of water, food and oxygen to habitats below the dams.

Alasmidonta heterodon, *Anodonta imbecillis*, *Pleurobema brimleyi*, *Elliptio productus* and *Lampsilis ochracea* occurred only below dams. The few previous basin records suggest that these are the only currently suitable sites. C. S. Brimley[2] recorded *A. heterodon*, *A. imbecillis*, *E. productus*, *Ligumia constricta*, *L. delumbis* and *Lampsilis conspicua* from the Neuse near Raleigh, but the author did not find them there. *Pleurobema brimleyi* was not found in Walnut Creek from which Brimley noted that it was described (see Simpson, 1914: 805). That areas below dams offer more nearly optimum habitats appears from the larger numbers of species and individuals, e.g. 39 *E. complanatus* at station 18, 14 *E. complanatus roanokensis* and 64 *Lasmigona subviridis* at station 45. Stations 5 and 6 are below dams. Since species common to both were more abundant, and there were two more species (total, six) at station 5, a cumulative effect is indicated, i.e. two dams are better than one. In the steep 15 miles from the station 50 dam to station 45 below Milburnie, species number doubles to four.

Teleodesmacea.—In the estuary below New Bern, young *Polymesoda caroliniana* were found in intertidal zone sandy clay with small, embedded twigs. A coastal or near-coastal sphaeriid, *Eupera cubensis*, occupied muddy sand in slow, shallow water a few miles upstream from New Bern. Other sphaeriid occurrences were erratic, showing no correlation with factors found important to snails and unionids.

Relationships of mollusks and pollution are discussed by Baker (1901, 1922), Ellis (1931), Ellis *et al.* (1931), Van Cleave (1940) and others. Neuse Basin cities, except Durham, discharged untreated domestic and industrial wastes into the Neuse (Stiemke, 1947). In this study, sludge was conspicuous below Raleigh at Walnut Creek station 30, slight at Crabtree Creek station 34. Biological oxygen demand (B.O.D.) measurements, supplied by the state Stream Sanitation Commission and the Durham Water and Sewer Department, extend discontinuously from early 1944 to late 1953 and from close above Ellerbee Creek to Smithfield. Taking a B.O.D. of a 2.5–5.0 p.p.m. to indicate heavy pollution, of over 5.0 p.p.m. as gross, then the limited number of data signify heavy to gross pollution.

Below effluent discharges into the Neuse, apparently suitable spots showed

[2] Remarks about C. S. Brimley in this paper derive from an unpublished, partly annotated card catalogue of North Carolina mollusks. This appeared to be based on the literature and personal collecting, and was kept in the Division of Entomology office, State Agriculture building, Raleigh.

absences or small numbers of several species. This was most striking below station 45. *Clappia virginica* and *Menetus dilatatus* were absent from above Crabtree Creek to station 27, some 22 river-miles. *Mudalia carinata*, however, was present at station 33 below the mouth of Crabtree Creek in a recovery zone, according to Campbell (1939). It was absent from there to station 27. Others not found below the mouth of Walnut Creek for varying distances were *Ferrissia hendersoni* and *F. diaphana*, *Lasmigona subviridis*, *Alasmidonta undulata*, *Elliptio complanatus* and *E. complanatus roanokensis*.

Most of the distributional gaps above Raleigh extended from the Flat and Eno-Little drainages to at least eight miles below Ellerbee Creek. The treated wastes of Durham and the untreated wastes of the Camp Butner area entered this reach of the river via Ellerbee and Knap of Reed Creeks respectively. Found here were only *Lasmigona subviridis*, *Physa inflata*, *Fossaria modicella*, and *Amnicola limosa*, although others were in tributaries. *Menetus dilatatus* and *F. hendersoni* were at station 68 in Ellerbee Creek below the sewage treatment plant, but they occupied shallow riffles, not the usual, calmer, deeper waters. At riffle-station 117 below Hillsboro, *C. virginica* and *M. dilatatus* were not among the several species present, but both occurred above and below this point. *Menetus dilatatus*, having been at station 68, may not be too sensitive to pollution moderated by distance or treatment, but *C. virginica* was never found close below a known source of pollution.

DISTRIBUTION. *Unionidae and Stream Types.*—In eastward draining streams from Virginia to New York, Ortmann (1913) found a fauna of rather uniform size from lower to upper river, but one which diminished sharply in the headwaters. In the fauna of those streams most mussels had a more or less continuous occurrence. Widely varying water levels, silting and pollution may have altered the original, unknown molluscan fauna of the Neuse River Basin. In the modern state, only three naiads occupied over six stations in the entire basin, quite a different distribution from that found by Ortmann to the north. That the most widely distributed mussel is the adaptable *Elliptio complanatus*, and that others have so few stations, indicate that conditions are unfavorable to less adaptable forms often enough to prevent their establishment or spread.

Unionid-occupied stations were assigned to serial stream types based partly on widths and depths. To these were added the species and the number of stations at which each occurred in each type (Frequencies, Table I). The result is a distribution pattern confirming that reported by Ortmann (1913) for Atlantic drainages. That such manipulation of the data is necessary to uncover this pattern probably means that the modern fauna is reduced in number of individuals, if not of species. From medium-sized rivers to large creeks, the species-number is about seven, although species-composition changes. In small creeks the fauna is almost halved and frequencies are lower. Lower and large river species-number would be of the same order as the above if six mussels reported from other parts of the Coastal Plain had been present. These are: *Strophitus undulatus; Lasmigona subviridis; Alasmidonta undulata; Anodonta cataracta; Ligumia delumbis; Lampsilis ochracea.*

TABLE I

Distribution and frequencies of unionids by stream types

Type	Species	Frequencies	Stations
1. Small creeks	*Strophitus undulatus*	1	14, 22, 24, 37, 40, 43, 57, 76, 82, 115, 123
	Lasmigona subviridis	2	
	Elliptio complanatus	9	
	Ligumia constricta	1	
Totals	4		11
2. Large creeks	*Strophitus undulatus*	3	15, 17, 18, 20, 38, 42, 80, 81, 86, 101, 104, 120, 122
	Lasmigona subviridis	4	
	Alasmidonta undulata	2	
	Anodonta imbecillis	2	
	Elliptio complanatus	11	
	Ligumia constricta	4	
	Ligumia delumbis	1	
Totals	7		13
3. Small rivers	*Lasmigona subviridis*	3	2, 5, 6, 78, 88, 107, 113
	Alasmidonta undulata	1	
	Alasmidonta heterodon	1	
	Pleurobema brimleyi	1	
	Elliptio complanatus	7	
	Elliptio productus	2	
	Ligumia constricta	3	
Totals	7		7
4. Medium-sized rivers	*Lasmigona subviridis*	4	8, 47, 56, 77, 110, 112, 117
	Pleurobema brimleyi	1	
	Elliptio complanatus	5	
	Elliptio complanatus roanokensis	1	
	Ligumia constricta	1	
	Lampsilis ochracea	1	
Totals	6		7
5. Large rivers	*Lasmigona subviridis*	5	25*, 26*, 27*, 33†, 45, 49, 50
	Alasmidonta undulata	3	
	Elliptio complanatus	5	
	Elliptio complanatus roanokensis	4	
Totals	4		7
6. Lower river	*Elliptio complanatus*	2	130, 136‡
	Elliptio complanatus roanokensis	1	
Totals	2		2
7. Lake Michie	*Anodonta cataracta*	1	75 (impoundment)
	Elliptio complanatus	1	
	Lampsilis conspicua	1	
Totals	3		1

* Below mouth of Walnut Creek.

† Between mouths of Walnut and Crabtree Creeks.

‡ Only dead shells of both forms found, in dry mud on base of mid-stream bridge support.

More or less continuous occurrence from lower to upper river is shown by *Elliptio complanatus* (all stream types), *Lasmigona subviridis* (large rivers to small creeks) and *Ligumia constricta* (medium-sized rivers to small creeks). Since *A. undulata* was in large and small rivers and large creeks, it probably occurs in medium-sized rivers. Those species already noted as once, but no longer, found in the Neuse are limited to one or two stream types, e.g. *Anodonta imbecillis. Elliptio complanatus* was the most common and widespread species in all stream types but large rivers where *L. subviridis* equalled its frequency, surpassed it in numbers of individuals. *Ligumia constricta* and *A. undulata* were next most common.

Upper versus Lower Basin.—Of the 14 stations considered to be in the Coastal Plain, 11 are in the lower basin and may be an inadequate sample. However, the fairly uniform findings seem to justify their use in a small-scale comparison.

Unionids, and branchiate and small pulmonate snails are wholly or largely restricted to the upper region of the basin, chiefly to streams larger than small creeks. The upper Coastal Plain stations (2, 25, 26) are some distance from known pollution sources. They may be under Fall Zone influence and, therefore, transitional. At any rate, their fauna (14 spp.) is larger than that of the lower basin stations.

Omitting the dead *Valvata bicarinata*, and coastal forms *Eupera cubensis* and *Polymesoda caroliniana*, leaves eight species found alive in the lower Neuse, 22 percent of the upper basin number. With tributaries, the figures become 10 species and 27 percent by adding *Campeloma decisum* and *Pisidium abditum* to: *Amnicola limosa; Pseudosuccinea columella; Helisoma anceps; Ferrissia diaphana; Physa inflata; Elliptio complanatus; Musculium contractum; M. partumeium.* Six mussels recorded from other parts of the Coastal Plain and which could conceivably have occurred here were listed in "Unionidae and Stream Types". Absence of the riffle-group was expected, but sites seemingly suitable for most other species were uninhabited.

Geographic Distribution.—The four riffle-dwellers, *Clappia virginica, Mudalia carinata, Oxytrema catenaria dislocata* and *O. proxima*, and *Ferrissia hendersoni* and *Physa inflata* are predominantly southern and eastern, the other snails occurring west of the Appalachians. *Clappia virginica* and *M. carinata* range to Maryland and New York respectively, and *P. inflata* has been recorded from the French Broad (westerly) drainage.

Lasmigona subviridis and *E. complanatus* occur to a limited extent beyond the Atlantic drainage which, however, is their center and over which they range generally (Ortmann, 1913). Likewise, *Anodonta imbecillis* and *Ligumia constricta* occur west of the Appalachian divide, but they are southern in the eastern drainage (Simpson, 1914). Other Atlantic drainage species of southern range are: *Elliptio productus; Pleurobema brimleyi; Ligumia delumbis; Lampsilis conspicua.* Also of general range are: *Alasmidonta undulata; A. heterodon; Anodonta cataracta; E. complanatus roanokensis. Strophitus undulatus* and *Lampsilis ochracea* are of northern distribution.

Most of the freshwater sphaeriids range widely in the United States (Sterki, 1916); for *Musculium contractum* only southern records were found.

Physiographic Distribution.—The provinces occupied in the Neuse Basin are those occupied elsewhere as determined from literature and museum records and by basin limits. Branchiates and small pulmonates occur in the Piedmont and Fall Zone, whereas the three large pulmonates occur also in the Coastal Plain. The known ranges of *Ferrissia diaphana* and *Physa inflata* extend now from the mountains to the Coastal Plain, while those of *Menetus dilatatus* and *Ferrissia hendersoni* extend from the Coastal Plain to the Piedmont. Six naiads (*Lasmigona subviridis; Alasmidonta undulata; Anodonta cataracta; Ligumia delumbis; Strophitus undulatus; Lampsilis ochracea*) which have been recorded from other parts of the Coastal Plain were not found there in the Neuse Basin. The last two, Piedmont forms here, are estuarine to the north (Ortmann, 1919). The few stations of most of the unionids limited them to a part of their reported physiographic range.

SUMMARY

(1) A survey of the Neuse River Basin yielded seven species of ctenobranchiate and seven of pulmonate snails; 14 of unionid and 11 of teleodesmacean mussels. (2) Known ranges of 15 species have been expanded, ten within, five into, North Carolina. (3) *Clappia virginica, Mudalia carinata, Oxytrema catenaria dislocata* and *O. proxima* composed an upper basin riffle-group; *Campeloma decisum* occurred throughout the basin in moderate to fast waters. (4) Pulmonata inhabited slow to moderate waters. *Menetus dilatatus, Ferrissia hendersoni* and *F. diaphana* were upper basin leaf-dwellers; *Pseudosuccinea columella, Helisoma anceps* and *Physa inflata* occupied the entire basin in individual habitats. (5) Most unionids occupied moderate to fast upper basin waters; *Anodonta cataracta* and *Lampsilis conspicua* were lacustrine. (6) Areas below dams were richer in unionid individuals and species, some of which may be relicts. (7) Branchiates and small pulmonates were absent or fewer below effluent outlets. (8) Assigning unionid-occupied stations to serial stream types revealed a distribution corresponding to that of other Atlantic drainage streams. (9) Species-number in the lower basin was about 75 per cent less than in the upper. (10) *C. virginica, M. carinata, O. catenaria dislocata, O. proxima, F. hendersoni* and *P. inflata* have a mostly southern and eastern distribution. *Strophitus undulatus* and *Lampsilis ochracea* are of northern range. *Elliptio productus, Pleurobema brimleyi, Lampsilis conspicua, Ligumia delumbis, L. constricta* and *Anodonta imbecillis* are southern ranging forms; the last two occur also west of the Appalachian divide. *Alasmidonta undulata, A. heterodon, Anodonta cataracta, E. complanatus roanokensis, E. complanatus* and *Lasmigona subviridis* are widely ranging species of the Atlantic drainage, but, again, the last two occur on the west side of the divide. (11) Generally, the same physiographic ranges are occupied here as in other parts of the Atlantic drainage, but six naiads which might have occurred in the Coastal Plain were not found. The known physiographic ranges of *M. dilatatus, F. hendersoni, F. diaphana* and *P. inflata* have been expanded.

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A MARKED ALIGNMENT OF EARTHQUAKE EPICENTERS IN WESTERN NORTH CAROLINA AND ITS TECTONIC IMPLICATIONS

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In the early morning hours of September 28, 1956 a small earthquake shook up an area of more than 1700 square miles near the common corner of Ashe and Allegheny Counties, N. C., and Grayson County, Va. It was felt by many persons in the affected area, a fair proportion of whom were awakened by the vibrations, and was recorded by the seismograph operated in Chapel Hill by the University of North Carolina, but seems to have done no damage.

While working out the details of this earthquake it was noticed that its epicenter (center of the disturbed area) fell not far from, and exactly in line with, the epicenters of two other recorded earthquakes: one in Watauga Co., N. C., on August 6, 1885, and one near Wytheville, Va., on October 21, 1897.

Further search of our earthquake records disclosed the fact that not only these three quakes, but at least eight others as well, fall along an almost perfectly straight line trending in a northeasterly direction across western North Carolina and on up into Virginia.

Figure 1 shows a crude sketch map of the general area, including the foot of the Blue Ridge Scarp according to William A. White, together with the approximate epicenters of these eleven earthquakes. Of course there have been numerous other small earthquakes in western North Carolina, so that perhaps I may with some justification be accused of "special pleading" in picking out this one small group for individual consideration. Nevertheless, they form such a clear-cut linear series that I cannot help feeling that they represent a real tectonic alignment—a belt of structural weakness in the uplifted Blue Ridge mass. It seems most probable that we are dealing with a more or less continuous zone of faulting; less probably with an individual fault of considerable strike

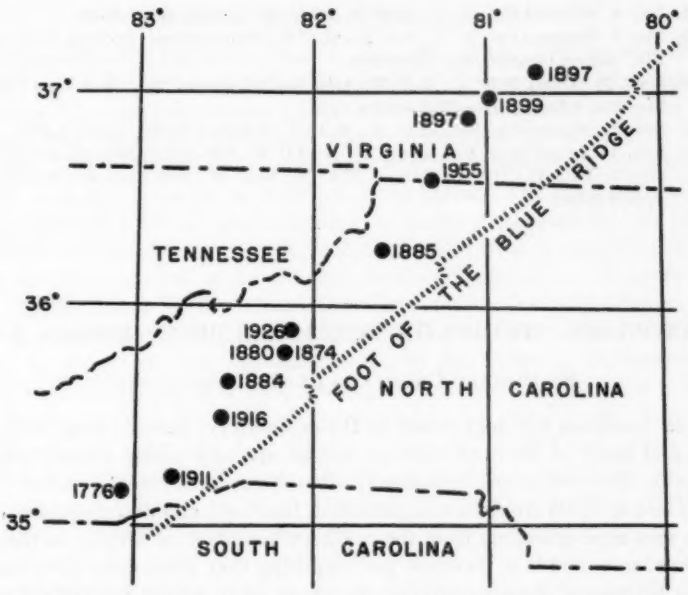

FIG. 1. The alignment of earthquake epicenters and the position of the Blue Ridge Front, the latter according to Wm. A. White.

length. In any event, we seem to have a zone of weakness, with numerous small movements which, from time to time, give rise to rather localized tremors and disturbances.

The alignment is roughly parallel to, but a few miles west of, the Blue Ridge Front (Fig. 1). Thus, while it cannot very well be *the* Blue Ridge Fault postulated by White[1], it could very easily represent a parallel zone of tectonic movement, related genetically to the greater fault which White believes to mark the foot of the Blue Ridge Escarpment.

Some details of these earthquakes, from south to north, are as follows:

1776: Night of Nov. 5-6. Jackson Co., N. C. "Severe shock of an earthquake which surprized our men very much." Between Tuckasegee River and Richland Creek, near Haywood Co. border.

1911: Apr. 21. Near Hendersonville, N. C. Affected about 600 square miles; felt rather strongly near Hendersonville.

1916: Feb. 21. Near Skyland, N. C., 35½° N., 82½° W. Affected 200,000 square miles.

1884: "Summer." Reported from Elk Mountain, just northeast of Asheville, near 35°40′ N., 82°30′ W. Similar to shock of Aug. 6, 1885.

1874: Feb. 10 through Apr. 17. McDowell Co., N. C. A series of 50 to 75 *local* shocks.

1880: Jan. 28, 29; Feb. 10. A minor repetition of the above series, centering at exactly the same place.

[1] White, Wm. A. 1950. The Blue Ridge Front—a fault scarp. Bull. Geol. Soc. Amer. 61: 1309–1346.

1926: July 8. Mitchell Co., N. C., 35.9° N., 82.1° W. A weak, local shock.
1885: Aug. 6. Watauga Co., N. C., 36.2° N., 81.6° W. Felt at Boone, Blowing Rock, Banner Elk, and on Grandfather Mountain.
1955: Sept. 28. About 36.6° N., 81.3° W. Ashe and Allegheny Cos., N. C., and Grayson Co., Va. Affected over 1700 square miles.
1897: Oct. 21. Wytheville, Va., 36.9° N., 81.1° W. Affected 20,000 square miles.
1899: Feb. 15. Lynchburg, Va., about 37° N., 81° W. Affected 30,000 square miles.
1897: May 3. Pulaski City, Va., about 37.1° N., 80.7° W. Felt over an area of 150,000 square miles.

TAXONOMIC STUDIES ON NORTH AMERICAN MOSSES. I–V.[1]

BY HOWARD CRUM[2] AND LEWIS E. ANDERSON[3]

North American bryology is still in the exploratory, floristic stage of development, and many of the most common species are very poorly understood, taxonomically, floristically and ecologically. It was not until recently, when Grout's *Moss Flora of North America* was published, that keys and descriptions of mosses of the vast area extending from the northern boundary of Mexico to the Arctic were available, and it is therefore not surprising that bryologists have been few or that taxonomic investigations in the Musci have lagged far behind interest in the phytogeography and cytology of the group, to mention only two of the fields of study that have recently come into prominence in North America.

It is to be expected that a pioneer work of broad scope such as Grout's *Flora* should have its faults. Dr. Grout himself freely admitted as much but justified its publication, and rightly so, as providing a foundation for further study. Fortunately the work is rather well documented, and because it was compiled, for the most part, by Dr. Grout and his students, most of the errors found therein can be amended by reference to Grout's herbarium at Duke University. The herbarium consists of a large collection of dried specimens as well as a valuable set of study slides from which Grout developed his concepts. Much of the present work is based on studies of these specimens and slides.

In the preparation of this paper we have been able to work together on two different occasions at the Grout Herbarium, and we have also studied all the pertinent material in the National Museum of Canada and the American Bryological Society Herbarium at Duke University. We are grateful to Dr. E. B. Mains (University of Michigan) and to Dr. Robert F. Thorne (State University of Iowa) for the loan of specimens of *Gyroweisia* not otherwise available to us. We are greatly indebted to Mr. Thomas M. Simkins, Jr., Duke University Library Staff, for his aid with the Latin diagnoses.

[1] Published by kind permission of the Chief Curator of the National Museum of Canada.
[2] National Museum of Canada, Ottawa, Ontario.
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I. *GYMNOSTOMUM* IN NORTH AMERICA

Both *Gymnostomum calcareum* Nees & Hornsch. and *G. aeruginosum* Smith have been reported from most parts of North America, apparently wherever wet limestone or other calcareous rocks occur, and both are thought to be widespread in Europe, Asia, Africa and elsewhere. Badly confused in North America, they are at best weakly delimited by characters which are subject to considerable variation, no doubt associated with differences in habitat. Found on wet rocks or on rocks alternately wet or dry depending on seasonal fluctuations, the plants belonging to this complex vary in size, leaf shape and degree of papillosity of leaf cells in much the same way as do other species of similar habitat, such as *Gymnostomum recurvirostrum* Hedw., *Amphidium lapponicum* (Hedw.) Schimp. and *Eucladium verticillatum* (Brid.) Bruch & Schimp. The puzzling variation exhibited generally by mosses of very wet habitats is well illustrated in *Drepanocladus*, *Scorpidium* and *Calliergon*, and the polymorphic expressions of species of wet calcareous habitats, such as *Didymodon tophaceus* (Brid.) Jur. and *Barbula ehrenbergii* (Lor.) Fleisch., are notorious. Any attempt to sort the myriad and intergrading forms of such species into more than "phases" or "ecotypes" is not only difficult but probably also futile in any genetic sense, and no useful purpose is served by granting them formal recognition as forms.

The confusion and uncertainty regarding *Gymnostomum* in North America is well illustrated by a letter from Mr. E. B. Bartram, who said, "I have often wondered whether *G. calcareum* could not be aptly considered as a variety of *G. aeruginosum*. As far as the length of the stems is concerned there is certainly a broad twilight zone and after sifting the distinctions one has left only the relatively broader, more rounded leaf apex as a diagnostic marker. The extremes are well marked, but I rather think you will agree with me that there are many collections that can only be named with a query."

We have studied a large series of specimens referred to *G. calcareum* and *G. aeruginosum*, from both North America and the Old World, over a period of several years. We have come to the conclusion that nearly all the North American plants passing under the name of *G. calcareum* are forms of *G. aeruginosum* instead. Only from California have we seen a goodly number of specimens which can better be named *G. calcareum*, and even those seem doubtfully worthy of specific rank. We are hesitant to alter the taxonomic status of *G. calcareum* at this time, however, because the distinct range in North America suggests a genetic differentiation which can perhaps be demonstrated by cytological study or by physiological and ecological investigation.

Judging from European specimens available to us, we suspect that *G. calcareum* can be segregated rather well as a geographic race in the Mediterranean region but that northward in Europe the name may serve as little more than a "pigeon-hole" for extreme variants of *G. aeruginosum*, as it often has in North America. The disjunct occurrence of *G. calcareum* in California and Mediterranean Europe is not particularly surprising, as growth conditions are essentially similar and a number of other mosses follow the same pattern of disjunction, as do many flowering plants, some of them accidental introductions in California.

In typical form, *G. calcareum* has rather short, broad leaves which are scarcely tapered and usually end in a broad, rounded or rounded-obtuse apex. *G. aeruginosum*, on the other hand, typically has narrower leaves tapered to a narrow, acute or blunt apex. Furthermore, the cells of *G. aeruginosum* are usually more obscure. *G. calcareum* var. *intermedium* Schimp., in Europe, has ovate leaves tapered to a rather narrow apex, but in areolation as well as in relative breadth of leaves it seems referable to *G. calcareum*. In North America, *G. aeruginosum* varies greatly in leaf shape and in the angle of the leaf apex so that in practice plants with most leaves rather blunt have been referred to *G. calcareum*, and, conversely, those with a preponderance of acute leaves have been called *G. aeruginosum*. Usually, however, leaves of both types can be found on the same stems, and very often both plants with mostly acute leaves and others with mostly blunt leaves can be found in the same tufts. The obscurity of the leaf cells of *G. aeruginosum* seems to be associated in part with the degree of maturity. Younger leaves with smaller cells are relatively more obscure than fully developed leaves because they bear more papillae per unit area.

The confusion of *G. aeruginosum* and *G. calcareum* in North America can be attributed to mistaken concepts in the literature concerning *G. calcareum*, as well as to the puzzling variation exhibited by *G. aeruginosum*. For example, Steere's illustration (1939) of *G. calcareum* represents admirably our understanding of typical *G. aeruginosum* in the narrow leaves tapered to an acute, often apiculate apex, as well as in areolation. Jennings' illustration (1913) of *G. calcareum* closely approximates our concept of a common form of *G. aeruginosum* with narrow, bluntly pointed leaves but not the broadly ligulate and very broadly-pointed leaves of genuine *G. calcareum*.

Grout's treatment of the genus (1938) is quite unsatisfactory, on the generic as well as the specific level. We believe that *Hymenostylium* is a weak segregate and, therefore, agree with Grout's inclusion of *H. recurvirostrum* (Hedw.) Dixon in *Gymnostomum*, but we cannot follow his interpretation of *Gyroweisia tenuis* (Hedw.) Schimp. as a *Gymnostomum*, because of its differentiated perichaetial leaves and its very well developed annulus. We have seen the material of *Gyroweisia tenuis* from Manitoba and Michigan reported and illustrated by Steere (1939) and also that reported by Conard (1945) from Iowa. The plants from Owen Sound, Ontario (*E. A. Moxley*, May 24, 1934) seem to be correctly referred to as *G. reflexa* (Brid.) Schimp., as Conard indicated, and not *G. tenuis*, as previously reported by Steere, although the peristome teeth are not so well developed as those illustrated in Engler and Prantl's *Die Natürlichen Pflanzenfamilien* or exhibited in the limited number of European specimens which we have seen. It is clear, however, that *G. reflexa* is closely allied to *G. tenuis* and that *G. tenuis* is gymnostomous probably by reduction and actually belongs to a peristomate series rather than to *Gymnostomum*.

Grout's specific concepts were also confused, as shown by the exsiccati specimens which he cited as authentic. Among these attributed to *G. calcareum*, Bartram's *Mosses of Southern Arizona 134* is *Anoectangium obtusifolium* (Broth. & Paris) Grout; Grout's *North American Musci Perfecti 189* is fairly typical *G.*

aeruginosum and not at all similar to the specimen of *G. calcareum* var. *intermedium* distributed as Husnot's *Musci Galliae 552*, as Grout said; Holzinger's *Musci Acrocarpi Boreali-Americani 377* is a rather blunt-leaved form of *G. aeruginosum* (with the typically obscure leaf cells of that species); Drummond's *Musci Americani* (British North America) *21* has been referred by Steere (1939) to *Gyroweisia tenuis*. The following, cited as *G. aeruginosum*, show considerable variation but seem to us reasonably typical: Drummond's *Musci Americani* (*British North America*) *24*, Holzinger's *Musci Acrocarpi Boreali-Americani 3a*, *4* and *4a*, Sullivant and Lesquereux's *Musci Acrocarpi Boreali Americani* (ed. 1) *38* and *39*, Grout's *North American Musci Perfecti 179*, Bartram's *Mosses of Southern Arizona 88* and Austin's *Musci Appalachiani 60*. Austin's *61* is *G. recurvirostrum* (Grout was mistaken in stating that it was issued as *G. calcareum*). Holzinger's *Musci Acrocarpi Boreali-Americani 3* at Duke University is clearly *G. recurvirostrum* var. *scabrum* Lindb., while that at the National Museum of Canada is *G. aeruginosum*. Drummond's *Musci Americani* (*Southern States*) *21* and Austin's *Musci Appalachiani 62*, not cited by Grout, also belong to *G. aeruginosum*. Grout omitted mention of *Gymnostomum rupestre* var. *minor* Sull. & Lesq., issued (with a description) as *no. 51* of the second edition of the *Musci Boreali Americani*; it is a commonly encountered small form of *G. aeruginosum* quite similar to *Gymnostomum pusillum* Kindb., a Canadian species which we would refer to the synonymy of *G. aeruginosum* rather than to *G. calcareum*; this same form is found in Drummond's *Musci Americani* (*British America*) *23*, which Grout failed to cite.

Bartram (1949) has reported *Gymnostomum calcareum* from Guatemala, but one of the specimens which he cited (*Sharp 2441*) is a small form of *G. aeruginosum*, and we suspect that all the Guatemalan records can be similarly placed, as the extraneous temperate elements in Guatemala are largely eastern American in distribution or affinity and not Californian or even western American.

The specimens which Sharp (1938) reported from the mountains of North Carolina as *Anoectangium euchloron* (Schwaegr.) Mitt. are clearly referable to *Gymnostomum aeruginosum*. Both *Sharp 36217* and *3178* from Dry Falls near Highlands in Macon County have terminal female inflorescences (although they often appear lateral because of innovations), and for that reason alone cannot be placed in *Anoectangium*. These specimens show the usual variation in the angle of the leaf apex, even on the same stems, from obtuse to acute. The leaf apices are often tipped by a minute hyaline point, suggestive of the apiculus of *Anoectangium euchloron* but by no means so abrupt or pronounced. We are grateful to James Kucyniak for calling our attention to striking differences in the leaf sections of *Gymnostomum aeruginosum* and *Anoectangium euchloron*. The costa of the former has median cells of a moderate size and no stereid cells above them; that of the latter, however, has enlarged cells in a median row and stereids in a single layer above them. (The differences in costal structure have been illustrated in figures 1–2.) The discovery that these plants have been misdetermined is of more than casual interest, because *Anoectangium euchloron* has been considered one of a small number of local disjuncts restricted in eastern North America to

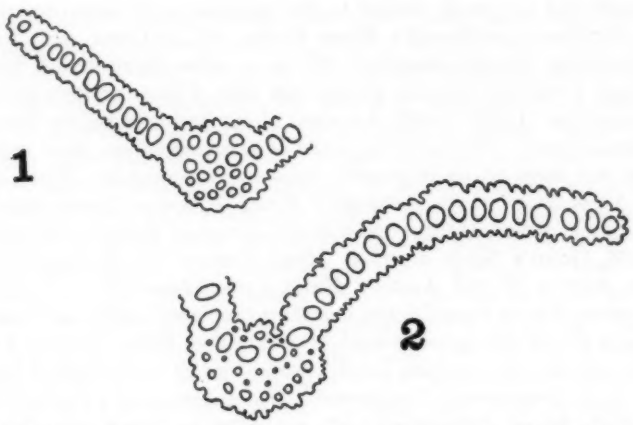


FIG. 1–2. A comparison of costal structures. FIG. 1. Cross-section through the leaf middle of *Gymnostomum aeruginosum*. × 440. FIG. 2. Cross-section through the leaf middle of *Anoectangium euchloron*. × 440.

the Southern Appalachian Mountains but widespread in the American tropics and thought to be relicts of a wider Tertiary distribution in temperate latitudes. (*Anoectangium euchloron* is found in Arizona; *Bartram 971* from the Patagonia Mountains of Santa Cruz County has been verified.)

II. *ORTHOTRICHUM EXIGUUM* SULL.

Orthotrichum exiguum is a very rare species which was described from material collected at Santee Canal, South Carolina, by Ravenel (Sullivant, 1864) and is known otherwise only from Norfolk, Virginia (*James*) and Georgia (*Lesquereux*). Recently we discovered a specimen from the Piedmont of North Carolina collected by Fred W. Gray at Marshville on March 4, 1931 (probably from the bark of an elm tree). Marshville is located in Union County near the Fall Line, at an altitude of about 550 feet. It thus appears from the few known collections that the species can be expected to occur more generally in the Southeast at lower elevations, either in the Coastal Plain or in the Piedmont.

O. exiguum is very curious in appearance and easily recognized even when sterile because of its delicate stature and its short, clavate stems and branches. Its leaves are appressed and not at all contorted when dry, very small and progressively larger toward the stem tips, thus accounting for the club-shaped stems; they are somewhat decurrent and more or less fimbriate at the base. The cells are bulging and bear several rather small C-shaped papillae; they are neither "minutissime papillosae," as Sullivant described them, nor "papillose-mammillose, the papillae nearly as large as the cell and sometimes slightly notched," as Grout said. A good and possibly constant diagnostic feature is provided by the numerous large propagula which occur on both surfaces of the leaves. The propagula are brownish, papillose, filamentous structures much like those of

Tortula caroliniana Andrews. Sullivant (1864) mentioned them rather casually as "excrescences" similar to those of *O. lyellii* Hook. & Tayl. (which are well illustrated in the *Bryologia Europaea*, fasc. 2–3, pl. 16). Grout overlooked the propagula of *O. exiguum* completely although they are present in a slide which he made from the type (Grout Slide Collection, Duke University); they are exceedingly abundant in Gray's collection from North Carolina.

Grout's treatment in his *Moss Flora of North America* and also in the *North American Flora* is misleading for several reasons. The plants, in North Carolina at least, are autoicous and not dioicous as both Sullivant and Grout believed. Although it is impossible to find antheridial buds on some plants, as many as two have been seen on some fruiting stems. Grout characterized the capsule as "obscurely ribbed when dry" and the exothecial cells as "not differentiated." In all the material examined, from Virginia, North Carolina and the type from South Carolina, we have found the capsules rather distinctly plicate (though not greatly constricted when dry) and the exothecial cells more or less differentiated in bands corresponding to the ribs.

The single specimen from North Carolina has sporophytes in rather poor condition. The endostome could not be found, but the shape of the urn, the nature of the exothecial cells, the position and appearance of the stomata and the shape and size of the peristome teeth agree perfectly with the type and conform to descriptions in the literature in all essential details. The markings on the peristome are rather puzzling, however. The North Carolina specimen shows teeth which are finely cross-striolate below and finely papillose above. The Virginia specimen, however, has a network of fine striae rather than discrete papillae above. The peristome in the type could not be examined, and the available descriptions, as well as Sullivant's illustrations (1864, pl. 35) give no information on the sculpturing of the exostome. In view of the distinct nature of the plants, as compared with other American species, and the many points of similarity among all the specimens examined, we believe that the peristome markings must be considered variable and probably of little specific significance.

It should be noted that the calyptra (which is naked except for a few hairs near the tip) is very finely roughened by small papillae borne singly on the cell lumina (and not mere projections of the cell ends). We have not noticed such papillae on the calyptrae of other *Orthotricha*.

Although we have not seen a sporophyte with the endostome intact, we did observe a fragment of a broad segment in the Virginia specimen which leads us to believe that Sullivant's description of eight segments broader than the teeth may be correct. Such a well developed endostome is unusual in the genus.

The North Carolina specimen contains, in addition to *O. exiguum*, an admixture of *Tortula pagorum* (Milde) DeNot.

III. **Orthotrichum keeverae** sp. nov.

Planta autoica, parva, rigida, sordido-viridis vel fulva, apice lutea. Caulis 0.5–1.5 mm. altus, furcatus, et, si siccus, curvatus. Folia 2–3 vel 3.5 mm. longa, et, si sicca, rigida imbricataque, sed, si madida, erecto-patentia vel patentia, oblongo-lanceolata, carinata, acuta, apice pleurumque longe cuspidata, margine

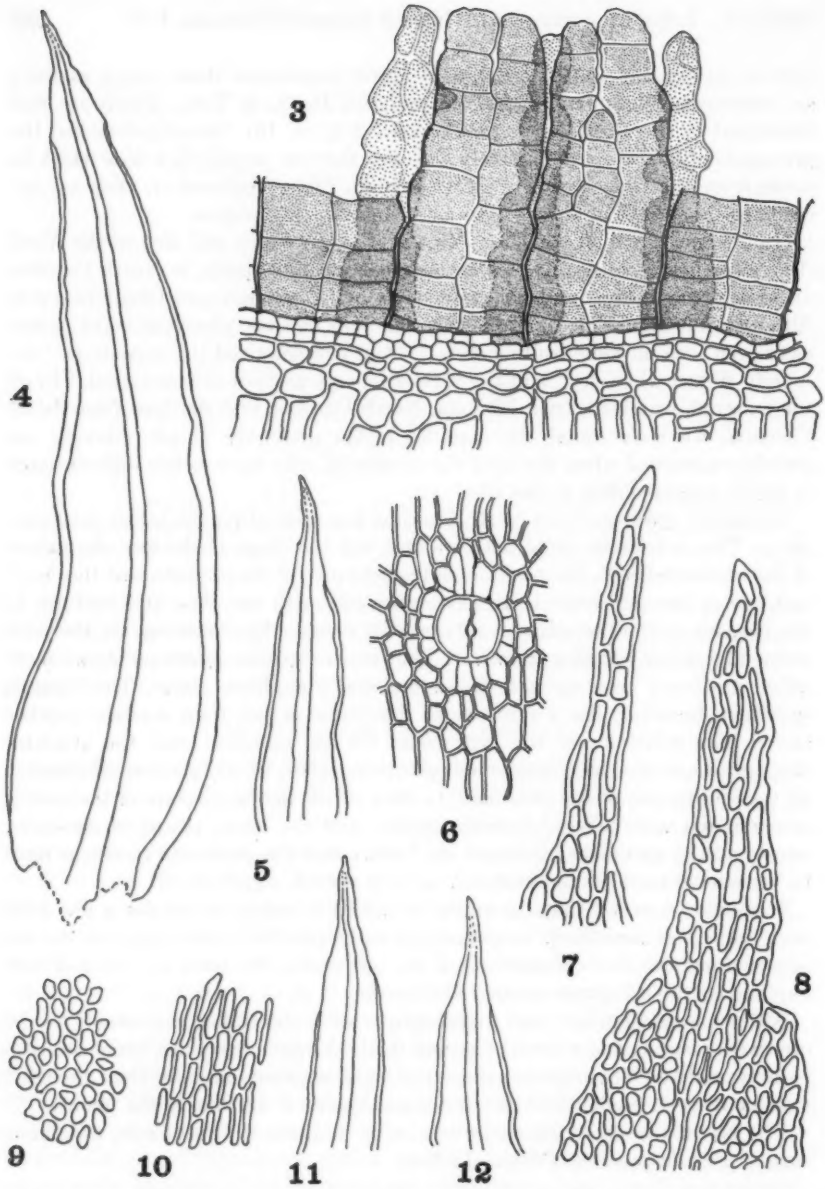


FIG. 3–12. *Orthotrichum keeverae* Crum and Anderson. FIG. 3. Portion of peristome and exothecium, showing two entire teeth of the exostome and two partially cut teeth showing the nature of the endostome. × 200. FIG. 4. Outline of stem leaf. × 48. FIG. 5. Outline of leaf apex. × 48. FIG. 6. Stoma, showing surrounding border cells and a portion of the exothecium. × 200. FIG. 7–8. Two leaf apices showing variation in angle and the leaf areolation. × 200. FIG. 9. Median leaf cells. × 200. FIG. 10. Median cells from the base of the leaf. × 200. FIG. 11–12. Outlines of leaf apices showing variations in angle. × 48.

fere usque ad apicem revoluta, superne subsinuata, cellulis superioribus 8–14 μ, irregulariter rotundatis, leniter papillosis; costa percursa vel in apice evanida. Capsula emergens, fulva, et, si sicca, longo-cylindrica et valde costata, saepe sub ore plus minus constricta sed non strangulata, cellulis costarum incrassatis in 8 seriebus dispositis; stomata phaneropora; peristomium duplex, infra orificium insertum; membranum basale altum et dentes 16 recurvi si sicci, pallido-fulvi, dense papillosi, apicibus truncati, endostomii processus 16, dentibus latitudine et plerumque longitudine aequales, validi, subrubro-brunnei, dense papillosi, lanceolati, marginibus irregularibus, et, si sicci, in cono dispositi sed non apicibus confluentes; operculum hemisphericum, subito rostratum. Sporae (25) 27–30 (32) μ, sphericae, dense et minutissime papillosae. Calyptra pilosa.

Plants small and coarse, sordid-green or brownish, yellow at tips. Stems 0.5–1.5 mm. high, forked, curved when dry. Leaves 2–3 or 3.5 mm. long, rigid and appressed when dry, erect-spreading or widely spreading when moist, oblong-lanceolate, usually contracted to a long-cuspidate point, slenderly acute, keeled; costa percurrent or disappearing in the apex; margins revolute nearly to apex, often irregularly notched or somewhat sinuate near apex; upper cells 8–14 μ, irregularly rounded, evenly incrassate, lightly papillose. Autoicous. Capsules emergent, brownish, elongate and cylindric when dry, strongly plicate, often somewhat contracted below the mouth but not strangulate or flaring at mouth; exothecial cells well differentiated in bands of thick-walled cells in 8 (often indistinct) rows, stomata superficial, below middle of urn; peristome double, inserted below the mouth, basal membrane high, the teeth 16, truncate, densely papillose, very pale brownish, recurved when dry, the segments of the endostome 16, well developed and dark brown, about as wide as the teeth and usually as long, densely papillose, lanceolate with irregular margins, directed inward to form a cone but not fused at tips; operculum hemispheric and abruptly rostrate. Spores (25) 27–30 (32) μ, spherical, very finely and densely papillose. Calyptra pilose. (Fig. 1–10).

Bark of *Quercus montana*, 1812 ft. alt., Rocky Face, Brushy Mts., near Hiddenite, Alexander Co., N. C., *Lewis E. Anderson & Catherine Keever 7575* (type in herb. Duke University); *7586*, June 21, 1948.

O. keeverae is erected as a new species because of its long-cuspidate leaves and the unique structure of its peristome. It is inserted below the mouth, and the exostome is only partially divided so that the teeth arise from a high basal membrane; the teeth are broad and not at all tapered to the truncate apex. When dry they are merely recurved or rolled backward rather than strongly reflexed against the outer wall of the urn in the manner exhibited by species with teeth inserted at the mouth and split to the base. The pale color of the exostome contrasts strongly with the dark brown endostome consisting of segments as well developed as the teeth and directed inward to form a cone. (The rolling of the teeth and the conical arrangement of the segments are approximated in the illustrations of *Orthotrichum callistomum* Fisch. *ex* BSG in the *Bryologia Europaea*, fas. 2–3, suppl. 2; the segments are not, however, fused at their tips as in *O. callistomum*.) *O. keeverae* is probably most closely related to a small group of species characterized by their well-developed endostomes; in North America this group is represented by *O. speciosum* Nees, *O. elegans* Hook. & Grev., *O. lyellii* Hook. & Tayl. and *O. exiguum* Sull.

Other bryophytes growing intimately with *O. keeverae* are *O. ohioense* Sull.

& Lesq., *O. stellatum* Brid., *Leucodon julaceus* (Hedw.) Sull., *Drummondia prorepens* (Hedw.) Jenn., *Ulota crispa* (Hedw.) Brid., *Frullania eboracensis* Gottsche and *F. squarrosa* (R. Bl. & N.) Dum.

It is a pleasure to name this unique species in honor of Dr. Catherine Keever, whose floristic and ecological studies in the Brushy Mountains and later pioneering successional studies have earned her a notable place in American ecology.

IV. The "Orthotricha straminea" of Eastern North America

Species of *Orthotrichum* are often separable only on the basis of small and intangible differences which may be exceedingly difficult to describe or to present in a key, but the additive effect of such differences may be such a distinctive expression that the species may be recognized at sight. Such is the case in the "Orthotricha straminea," which Brotherus (1925) treated as a subsection of the Euorthotricha. Grout (1946) recognized six species in the North American flora (in sect. Calyptoporus subsect. Straminea). (Two of them are western and have not been studied in detail, partly for want of adequate specimens: *O. pallens* var. *parvum* Vent. is immediately distinguishable by its stomata which are only slightly sunken and therefore nearly phaneropore; *O. garrettii* Grout & Flowers, a possible synonym of *O. canum* Mitt., according to Grout, 1935, appears to be more nearly related to the other American species in having fully immersed stomata.) The eastern American members—*O. pusillum* Mitt., *O. pumilum* Dicks., *O. stellatum* Brid. and *O. ohioense* Sull. & Lesq.—are widespread and form a homogeneous series of closely related species. They are small, autoicous, corticolous plants with emergent, slightly to strongly ribbed capsules, exothecial cells differentiated in longitudinal bands of thick-walled cells, stomata near the middle of the urn and immersed in cavities partly covered by projecting ends of surrounding cells and peristome teeth densely and finely papillose. The peristome is strongly reflexed in all but *O. pusillum*, in which it may become more or less recurved in extreme age.

The species have been greatly confused with one another, and Grout's descriptions fail to show their differential features, but in spite of their general similarities and some variation they can be recognized easily according to the following key and diagnoses:

Capsules nearly smooth to slightly plicate when old and empty; exothecial cells usually rather poorly differentiated in longitudinal bands; peristome teeth split into 16 irregular divisions, erect or occasionally becoming recurved with age ..... *O. pusillum*

Capsules clearly plicate; exothecial cells clearly differentiated; peristome reflexed.

Exothecial bands 4 cells wide; cells surrounding stomatal cavities projecting at steep to vertical angles; peristome teeth 8, soon becoming partially split and later divided into 16 pairs ..... *O. ohioense*

Exothecial cells in bands 8 cells wide; cells surrounding stomatal cavities projecting nearly horizontally; peristome teeth 8, undivided.

Leaves rigid, brownish, entire; leaf cells rounded, evenly thick-walled; capsules greatly constricted when dry and empty, strongly strangulate below the flaring mouth ..... *O. stellatum*

Leaves typically soft, blackish or sordid-green, apiculate or toothed at apex; cells collenchymatous, usually broader than long; capsules only rarely much contracted and only occasionally more than slightly strangulate ..... *O. pumilum*

O. pusillum Mitt.

Leaves small and soft, dark green or blackish, broad and very obtuse, perichaetial leaves irregularly denticulate at tips; cells *ca.* 16 μ, collenchymatous, pellucid; capsules smooth or wrinkled to very lightly plicate, short, small-mouthed and not at all contracted below the mouth, pale and straw-colored; cells surrounding stomatal cavity not particularly jutting or strongly differentiated; peristome teeth split into 16 small, irregular divisions, usually erect but sometimes reflexed in age, densely and finely papillose, often opaque; exothecial cells obscurely to rather well differentiated in bands 4 cells wide. Propagula sometimes produced on the leaves.

Growing on bark of trees. The range given by Grout (1946) includes "New England to Florida, west to Illinois and Missouri." We have seen material from Georgia, Kentucky, Mississippi, Missouri, New Jersey, New York, North Carolina, Pennsylvania, South Carolina, Tennessee, Texas, Vermont and Virginia.

The capsules of *O. pusillum* are usually entirely smooth when dry, although capsules in which the upper portion is wrinkled or very inconspicuously ribbed can be found. Grout (1935, 1946) described the capsules as "subglobose to ovoid," but this is misleading for the urn is actually largest at the middle and tapers gradually to a comparatively small mouth and similarly toward the base to a point where it narrows abruptly to the seta. The capsule is thus best described as "barrel-shaped." This shape is unique among the four species described here. In *O. pumilum*, with which this species has been most often confused, the capsules are somewhat obovate when dry and distinctly ribbed throughout; usually the capsules of *O. pumilum* are slightly contracted below the mouth, especially when old, and taper gradually to the seta.

In *O. pusillum*, the exothecial cells are differentiated into ribs that are four cells wide, but the differentiated cells are difficult to see in surface view. A cross-section of the capsule wall, however, shows that they are nonetheless clearly differentiated and that their indistinctness is mostly visual and not entirely structural. The eight rows of cells in the ribs of *O. pumilum* are clearly apparent even in surface view. Grout's statement that *O. pumilum* and *O. pusillum* "intergrade in various ways so that some specimens may be referred to either equally well" is incorrect and has doubtless contributed to the confusion.

An easily spotted diagnostic feature of *O. pusillum* is provided by 16 small, irregular peristome teeth which are erect or slightly recurved rather than reflexed as in the other species of this complex.

O. ohioense Sull. & Lesq.

Leaves rigid, brown, tapered to a rather narrow, blunt apex, entire; cells small, rounded, evenly incrassate, 9–11 μ, not noticeably translucent; capsules plicate but not greatly constricted, sometimes very slightly strangulate, short, abruptly or gradually narrowed to the seta, pale-brown; stomatal cavity surrounded by greatly differentiated cells with ends often jutting nearly vertically; exothecial cells rather distinctly differentiated into bands 4 cells wide; peristome teeth reflexed, 8, soon splitting into 2 lanceolate, regular divisions, finely and densely papillose, not obscure. Propagula apparently none.

On the bark of trees; "southeastern Canada and the eastern United States, south to Florida, west to Ohio and Ontario; Montana (according to O. Jennings, Mosses W. Pa. 120)" (Grout, 1946); we have seen material from Arkansas, Connecticut, D. C., Kentucky, Massachusetts, Michigan, Mississippi, New Hampshire, New Jersey, New York, North Carolina,

Nova Scotia, Ohio, Ontario, Pennsylvania, South Carolina, Tennessee, Vermont, Virginia and West Virginia.

Judging from the number of collections encountered, this is the commonest of the corticolous species in the eastern United States. It often grows with the other species, however, and the fact that it occurs in mixture with *O. pumilum* has certainly resulted in some confusion. Superficially, the capsules of *O. pumilum* and *O. ohioense* resemble one another in that when dry they are more or less cylindric and taper little or not at all toward the mouth. They are about the same color, and the ribs are often about equally prominent. In *O. ohioense*, however, the capsules rarely show any evidence of constriction below the mouth whereas capsules of *O. pumilum* are somewhat constricted (and occasionally even noticeably so). The two species are easily separated by the 4-celled ribs in *O. ohioense* and the 8-celled ribs in *O. pumilum*, a character which can usually be determined by viewing under a low power stereoscopic microscope. Under the compound microscope, the species are readily distinguished on the basis of leaf characters.

O. stellatum Brid.

Leaves rather rigid, brownish or yellowish, tapered, blunt or acute, entire; cells not pellucid, small and irregular, evenly incrassate, 9–12 μ; capsule elongate and tapered to the seta, strongly ribbed, strangulate, chestnut-brown; exothecial cells clearly differentiated in bands 8 cells wide, the cells below the suboral zone broad and thicker-walled; cells surrounding stomatal cavities clearly differentiated but projecting nearly horizontally, rather than steeply as in *O. ohioense*; peristome teeth 8, reflexed, rarely split, densely and finely papillose, not obscure. Propagula occasionally produced on the leaves; pale, brown, smooth, cylindric or shortly filamentous and quite similar to those found in *O. pusillum* and *O. pumilum*. (Propagula not yet discovered in *O. ohioense*.)

On bark of trees; "common in eastern Canada and the northeastern United States, south to Georgia, west to Iowa" (Grout, 1946); we have seen specimens from D. C., Indiana, Iowa, Kentucky, Maine, Massachusetts, New Hampshire, New Jersey, New York, North Carolina, Nova Scotia, Ohio, Ontario, Prince Edward Island, Québec, South Carolina, Tennessee, Vermont, Virginia and West Virginia.

This is the most distinctive and has been the least confused of the species under consideration here. The rather longer capsule, which is strongly ribbed throughout and conspicuously strangulate when dry, easily distinguishes this from the other species. The ribs are often tinged with a purplish pigment which contrasts strongly with the pale brown furrows between the ribs, and the result is a very attractive capsule.

The extreme constriction of the capsules is due to the fact that the differentiated rib cells are much thicker-walled where the constriction occurs at some distance below the mouth but become thinner-walled toward the middle of the capsule. Toward the mouth the ribs become gradually thinner and consist of fewer rows of cells, and this accounts for the flaring at the mouth of the urn.

Grout (1935, 1946) referred to differences in the hairiness of the calyptrae in these species, but we have found this character to be so variable as to be practically worthless and have not observed that the calyptra of *O. stellatum*, re-

ported to be hairless or nearly so, is actually any different from that of *O. ohioense* or *O. pusillum*.

O. pumilum Dicks.

Leaves typically soft, dark-green or blackish, obtuse or acute, apiculate or slightly toothed at extreme apex; cells 16–20 μ, rather pellucid, collenchymatous and usually broader than long; capsules oblong-ovoid, strongly plicate, contracted and usually somewhat strangulate when dry, occasionally strongly strangulate, dark brown; exothecial cells clearly differentiated in bands 8 cells wide, cells of rib not greatly incrassate below suboral zone as in *O. stellatum*; cells surrounding stomatal cavities rather variable, usually not greatly jutting or differentiated; peristome teeth 8, reflexed, densely and finely papillose, not particularly obscure. Propagula occasional on leaves.

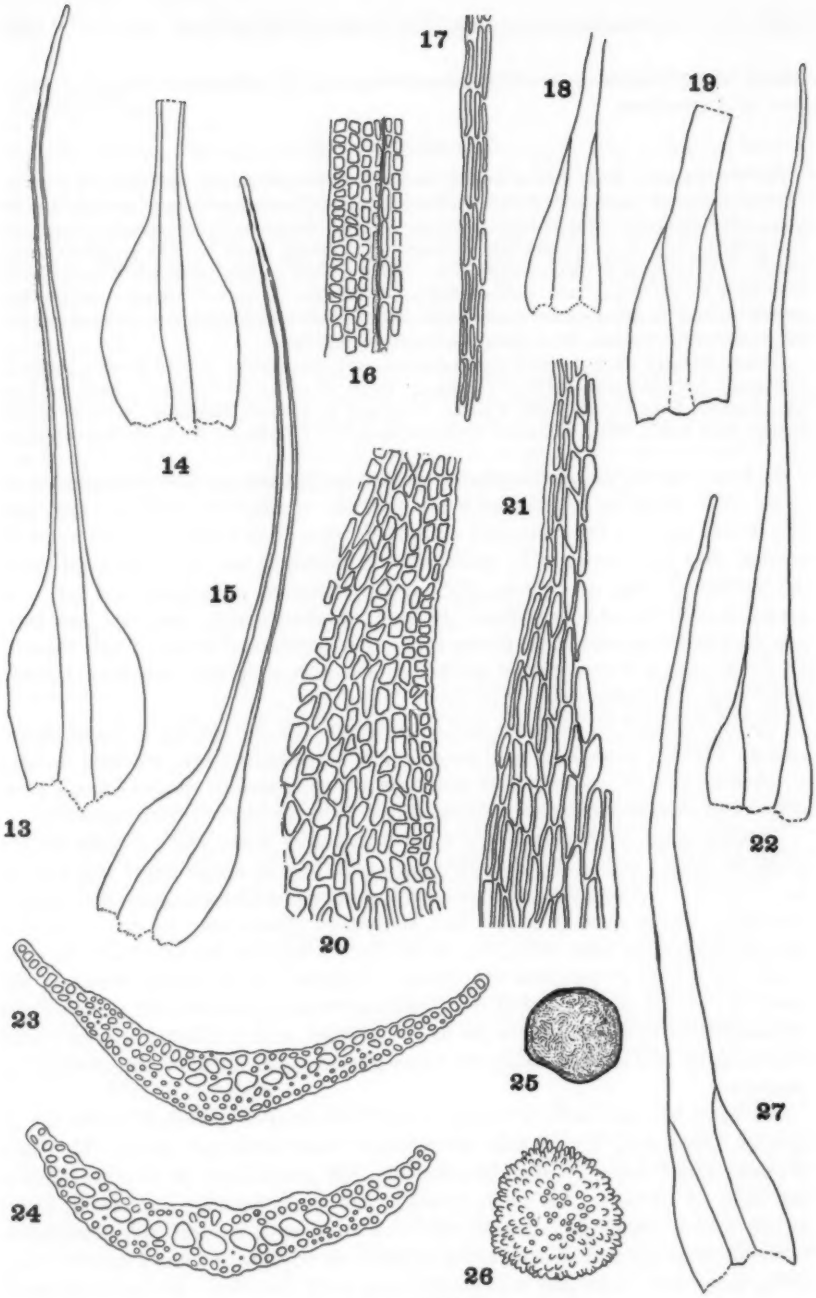
On the bark of trees, "southeastern Canada and the eastern United States, south to Tennessee, west to Idaho and Utah; Europe; Canary Islands; Asia" (Grout, 1946); we have seen material from Illinois, Iowa, Kansas, Michigan, Minnesota, Missouri, Nebraska, New Jersey, New York, North Carolina, Ohio, Ontario, South Dakota, Vermont and Virginia.

In total aspect, the gametophytes of *O. pumilum* bear a close resemblance to those of *O. pusillum* in that both are darkish- or blackish-green in color, and the leaves tend to be somewhat contorted when dry. Grout was incorrect in stating that the leaves of *O. pumilum* are imbricate and not contorted when dry (although they do occasionally appear somewhat more rigid and less contorted than those of *O. pusillum*). Both *O. pusillum* and *O. pumilum*, however, can always be spotted in mixtures with other species by virtue of this feature. In *O. ohioense* and *O. stellatum* the leaves are quite rigid and imbricate and not at all contorted when dry.

The leaf cells of *O. pusillum* and *O. pumilum* are also similar in being larger, clearer, broader than long and more or less collenchymatous, whereas in both *O. ohioense* and *O. stellatum* the leaf cells are significantly smaller, much more dense and obscure, irregularly rounded and more or less evenly incrassate.

The leaf apex of *O. pumilum* is characteristically acute and apiculate with a single elongated cell at the apex. We have been able to demonstrate this character in all of the North American material examined, although upper and slightly immature leaves show it to the best advantage. There may be one or several obscure serrations near the apex, or the leaves may be almost entire. In contrast, the leaf of *O. pusillum* tends to be lingulate and distinctly obtuse at the apex. All of the material of *O. pusillum* examined shows distinct serrations or denticulations at the apex of some leaves, at least, and in the majority of plants the toothing occurs in such a way as to give the leaf apex an asymmetric appearance.

We have not had sufficient material of European *O. pumilum* to render an opinion concerning its possible distinctness from American plants. This is a problem which urgently requires attention, but it will have to be considered in the light of at least two other possible European entities, namely *O. fallax* Bruch and *O. Schimperi* Hamm. We can state with considerable confidence, however, that the American material passing as *O. pumilum* has a narrow range of variation and in no way intergrades with other American species of the same general relationship.



FIGS. 13–26

V. Ditrichum henryi sp. nov.

Plantae autoicae, caespitosae, caespitibus laxis, humilibus, viridibus vel subflavis, nitidis compertae. Caulis 4–7 mm. altus, simplex. Folia superiore 4–5 mm. longa, et quotienscumque sicca erecta vel crispatula, non secunda, ad basim oblongo-ovata, plus minus subito canaliculato-subulata, marginibus ubique erectis, summo apice parce denticulatis, nervo lato et plano, percurrente, usque ad apicem lamina angustissima distincto, dorso laevi; cellulae basilares laxe oblongo-hexagonae, prope nervum latae, versus margines breviores et subquadratae, superiores breviores et incrassatiores, quadratae vel breviter oblongae, 7–14 × 7–8 μ. Folia perichaetii subvaginantia; androthecia plura. Seta (20) 25–35 (50) mm. longa, tenuis flexuosaque, lutea vel plus minus rubra; theca 2.5–3 mm. longa, suberecta vel inclinata paulo asymmetrica, ovato-cylindrica, ad orificium parvum attenuata, pallide fulva, et quotienscumque sicca et vacua plus minus sulcata; operculum 1.5 mm. longum, alte conicum, obtusum; annulus magnus, plerumque in fragmentis persistens; peristomium simplex, 1–1.3 mm. longum, dentibus 16, in basi coalitis, fere usque ad basim bifidis, ita ut 32 divisiones filiformes, spiculosas, pallide rubras, numerentur. Sporae 11–13 μ, sublaeves (minutissime reticulatae), flavae. Calyptra 4 mm. longa, cucullata, laevis.

Plants rather small, in low silky, green or yellowish tufts, or loosely gregarious. Stems 4–7 mm. high, simple. Upper leaves 4–5 mm. long, erect and somewhat crisped or contorted when dry, not secund, linear-subulate, rather abruptly widened below into a short, oblong-ovate base, channeled above with margins erect, slightly denticulate at extreme apex, smooth at back; costa broad and flat, percurrent, filling most of the subula; cells of leaf base laxly oblong-hexagonal, wide near costa and becoming shorter and subquadrate near the margins, just above the shoulders becoming shorter, thicker-walled and quadrate, upper cells quadrate or shortly rectangular, 7–14 × 7–8 μ. Autoicous; perichaetial leaves subclasping; perigonia numerous. Setae orange-yellow to reddish, slender and flexuous, (20) 25–35 (50) mm. long; urn of capsule 2.5–3 mm. long, suberect to inclined, slightly asymmetric, ovoid-cylindric, tapered to a small mouth, pale brown, indistinctly sulcate when dry and empty; operculum high-conic, blunt, 1.5 mm. long; annulus large and usually persistent in fragments; peristome teeth 16, split to a short membrane into 32 filiform, spiculose divisions, pale red, 1–1.3 mm. long. Spores nearly smooth, faintly reticulate at higher magnifications, 11–13 μ, deep yellow in mass. Calyptra cucullate, smooth, 4 mm. long. (Fig. 11–14, 18, 21, 23.)

On clay soil, road-cut, 2400 ft. alt., Upper Falls, Whitewater River, Jackson

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FIG. 13–27. *Ditrichum henryi* Crum and Anderson and *D. pallidum* (Hedw.) Hampe. FIG. 13–15. Leaf outlines of *D. henryi*. × 40. FIG. 16. Laminal cells of *D. henryi* midway between the base and the tip of the awn showing three rows of cells between margin and costa. × 200. FIG. 17. Marginal leaf cells of *D. pallidum* midway between the base and tip of the awn. × 200. (Note linear cells as compared with those of *D. henryi* in fig. 16. Drawings in both fig. 16 and 17 were made from the same relative positions of the leaf in the two species.) FIG. 18–19. Leaf outlines of *D. pallidum*. × 40. FIG. 20. Laminal cells from the leaf margin of *D. henryi* drawn from a point just above the shoulder of the leaf. × 200. FIG. 21. Laminal cells from the leaf margin of *D. pallidum* drawn from a point just above the shoulder of the leaf (to be compared with fig. 20). × 200. FIG. 22. Leaf outline of *D. pallidum* showing the broad costa which fills the awn. × 40. FIG. 23. Cross-section of the leaf of *D. henryi* taken at the point indicated in fig. 14. × 200. FIG. 24. Cross-section of the awn of the leaf of *D. pallidum* taken at the point indicated in fig. 19. × 200. FIG. 25. Spore of *D. henryi*. × 2000. FIG. 26. Spore of *D. pallidum*. × 2000. FIG. 27. Leaf outline of *D. pallidum*. × 40.

Co., N. C., *Lewis E. Anderson & Henry Wright 10014*, June 7, 1951 (type, in herb. Duke University); on open dry soil, Little Flat Rock, just east of Mt. Airy, Surry Co., N. C., *D. S. Correll & G. W. McDowell 10744*, May 25, 1939; on ground in Rock Creek Park, D. C., lat. 39° N., J. M. Holzinger, June 10, 1894 (Holzinger's *Musci Acrocarpi Boreali-Americani* 14, as *Ditrichum pallidum*), in part (specimen at National Museum of Canada, not the one at Duke University); on sandy soil, Jackson Township, Pike Co., Ohio, *Bartley & Pontius 3216*, June 7, 1942; on earth, sunny clearing, Kedji, Nova Scotia, *Margaret S. Brown 523*, Aug. 9, 1934.

The peculiar nature of *D. henryi* has been noted in the literature. Grout (1936) mentioned, as a variant of *D. pallidum*, specimens from Nova Scotia collected by Miss Margaret S. Brown with a longer oblong, clasping base with a larger number of small irregular cells at the leaf shoulders and a peristome rather more than 1 mm. long. Sharp (1939) reported collections "evidently representing a new species" from Van Buren Co., Tennessee, and also from Ohio. The Ohio specimen was referred to Grout who tentatively named it "*laevisporus* or var." (presumably of *D. pallidum*); it is *D. henryi*, but Sharp's Tennessee specimen is something else, not related to the present problem.

Ditrichum henryi and *D. pallidum* are very similar in appearance and on casual inspection are likely to be confused. They are, however, clearly distinct (particularly for a genus in which specific lines have often been drawn too closely for comfort), as illustrated in figures 11–25. The stem leaves of *D. pallidum* are narrowly ovate at the base rather than broadly oblong-ovate and obviously differentiated, and the perichaetial leaves are not or only slightly clasping at base. In *D. pallidum* the costa completely fills the subula for most of its length so that all the cells of the upper leaf are narrow and elongate. In *D. henryi*, on the other hand, the lamina is narrow but distinct to the apex of the subula or nearly so and consists of subquadrate cells; because the lamina is so very narrow, this character is most easily observed just above the leaf shoulders. Furthermore, the costa is very broad in the leaf base of *D. henryi*, but thin and indistinct in *D. pallidum*. The seta of *D. henryi* is orange-tinged or reddish and usually not likely to be confused in color with the pure yellow setae of *D. pallidum*. The capsules of *D. henryi* are somewhat smoother than in typical *D. pallidum*, although they are occasionally deeply furrowed when dry and empty, and *D. pallidum* also shows some variation in respect of furrowing of the capsule. The peristome teeth of *D. henryi* are rather uniformly 1–1.3 mm. long, whereas those of *D. pallidum* are generally less than 1 mm. long. The spores of *D. pallidum* are brownish in mass, papillose and 16–23 (rarely 27) μ; those of *D. henryi* are deep yellow in mass and very faintly reticulate, as viewed under high magnifications and only 11–13 μ.

There is also a clear chromosomal difference between *D. henryi* and *D. pallidum*. Bryan (1956) has reported that the haploid chromosome number of *D. pallidum* is 26, which is the same as that of *D. schimperi* (Lesq.) Paris, a closely related species of the Pacific Coast from California to British Columbia. Meiotic studies of material obtained from the type locality reveal that *D. henryi* has a haploid chromosome number of 13. It is of interest to note that in *D. curritucki* also, a close relative of *D. pallidum* confined to the Atlantic Coastal Plain, n =

13. The whole matter of polyploidy and geographic distribution in the genus *Ditrichum* has been considered by Anderson and Bryan (in press).

We have examined all the material filed as *D. pallidum* in the Grout Herbarium and the American Bryological Society Herbarium at Duke University and also that at the National Museum of Canada. From the few specimens of *D. henryi* found among them, we suspect the species to be northern and montane (or at least upland) in eastern North America. The plants from Washington, D. C., however, seem to be of doubtful origin; Holzinger's *Musci Acrocarpi Boreali-Americani 14*, distributed as *D. pallidum*, is obviously derived from more than one population and probably from populations of widely separated areas; the specimen at Ottawa is clearly *D. henryi*, while that at Duke University is *D. pallidum*. It is suspected that, because the two species are so similar in gross aspect and because *D. pallidum* is so common that it is generally named at sight rather than by careful microscopic study, Holzinger may have felt safe in "piecing out" his material with plants of *D. henryi* collected somewhere else.

This new species has been dedicated to Mr. Henry Wright, Field Naturalist for the Highlands Biological Station, Highlands, N. C. Mr. Wright, a lifelong resident of Highlands and a devoted and enthusiastic student of the outdoors, has served as guide, companion and observer for countless investigators in the Southern Appalachians. It is a pleasure, therefore, to associate his name with this handsome and distinctive species.

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NORTH AMERICAN LEJEUNEACEAE V. SCHIZOSTIPAE: CERATOLEJEUNEA[1]

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The genus *Ceratolejeunea* is a large and complex genus, developed primarily in the Neotropics. Only three species extend into the United States, and all three are restricted to the immediate Coastal Plain of the southeast. The genus has been admirably treated, as regards the Puerto Rican species, by Evans (1908), who has also described a species from the Bahamas (1911). More recently a partial revision of the genus has been published by Fulford (1945). The utility of this is impaired by the fact that although she states that 76 species are known from the New World tropics and subtropics, only 19 species are treated in her key, while a few others are eliminated by reduction to synonymy. Furthermore, it is impossible, in most cases, to gain from this key any concept of her ideas regarding the limits of the species, since most species appear at several points in the key (*C. maritima* appears five times; *C. valida*, three times; *C. plumula*, three times; *C. flagelliformis*, three times; *C. guianensis*, twice; *C. malleigera*, twice; *C. pungens*, twice, etc.). A third limiting element in this paper is the confusion introduced regarding the use of the name *C. guianensis*. Finally, Fulford was unable to arrive at any definite conclusion regarding the generic position of the holostipous species of *Ceratolejeunea*. As a consequence, the genus remains a fruitful subject for further systematic work.

In the present account, only the few North American species are treated. However, the introduction of two major new criteria, stem anatomy and extranuclear cytology, makes it possible to resolve some of the problems which remain, and to gain a more complete understanding of our regional species.

CERATOLEJEUNEA (Spruce) Schiffn.

Lejeunea subg. *Cerato-Lejeunea* Spruce, Trans. Bot. Soc. Edinburgh **15:** 198, 1884.
Ceratolejeunea Schiffner, *in* Engler-Prantl, Nat. Pfl.-Fam. **1**(3): 125, 1895; Evans, Bull. Torrey Bot. Club **32:** 273, 1905; Fulford, Brittonia **5:** 368, 1945.

Plants largely medium-sized to robust, the *shoots 0.8–2 mm. wide*, up to 5 cm. long, *shiny when dry, usually a clear, translucent brown to reddish-brown* (rarely merely bronzed, or deep brown), irregularly pinnate to plumose. Stem with pellucid, thin-walled *cortical cells in 7*

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[1] For a discussion of the Subfamily Schizostipae, and keys separating the genera, see the first article in this series (Jour. Elisha Mitchell Sci. Soc. **71**(1): 106–126, 1955, and, specifically, pages 118–124).

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The writer is now at the University of Michigan, Ann Arbor, Michigan.

rows (2 of which constantly form the ventral merophytes; these large, *ca.* 22–35 μ wide), the medullary cells thick-walled and much smaller, in *ca.* 20–22 rows. Leaves distant to weakly imbricate, in drying weakly convex to barely convolute; lobes ovate or ovate-triangular, rarely obovate, often slightly falcate, convex, the apices deflexed; the apex narrowly rounded to obtuse to acute, the *margin entire to crenulate or serrate, or more or less sharply toothed or incised*. Lobules *often dimorphic*: normal lobules usually ovate in outline, strongly inflated, the free margin usually involute to (or beyond) the apical tooth and appressed to lobe; *apical tooth 1-celled, usually sharp and pointed, the hyaline papilla at its proximal base, usually conspicuous*; keel usually strongly, convexly arched, usually ⅙–½ the length of the ventral lobe, with a generally sharp incision between apex of keel and the free posterior margin of dorsal lobe. In many species *with some leaves with isolated lobules much enlarged*, forming hemispherical to spherical water-sacs (utriculi), usually limited to 1 or 2 at the base of a branch. Cells *with walls usually strongly and evenly thickened*, the layer of thickening occasionally sinuous, except for scattered pits connecting the cells, at times with large triradiate trigones and intermediate thickenings (the "pits" or thin places then larger and less sharply circumscribed), with the walls usually pale brown, except for the *darker, deep-brown, conspicuous middle lamella*; *cells dimorphic*: a group of basal cells larger, more thin-walled usually, forming ocelli (usually 2–6 per leaf-base, more rarely extended as a short vitta; in one species the ocelli scattered, equal to surrounding cells in size); *ocelli each containing a single, large, usually homogeneous oil-body*; oil-bodies of vegetative cells *rather small*, usually linear to ovoid, *coarsely segmented, 3–5 per cell*. Underleaves moderate in size, 1.5–5 × the stem in diameter, *suborbicular, bifid* (except in 2 neotropical species), entire-margined, the lobes triangular, suberect. *Without specialized modes of asexual reproduction* (rarely with regeneration from leaf cells); in a few neotropical species reproducing by caducous leaves.

Autoecious or dioecious. Female inflorescence on long, leafy shoots, with 1 (rarely 2) subfloral innovations, which may again be floriferous. Bracts similar to leaves, the lobes similarly margined (margin entire to spinose-dentate or even laciniate); lobule explanate, lanceolate to ovate, *ca.* ½ the lobe in length; bracteole approaching underleaves in form, usually connate to bracts at base. Perianth *4-keeled* (2 lateral, 2 postical, 0 dorsal), the *dorsal surface plane*, the *keels typically extended* beyond the short beak *into* short or long, terete and longly tubular to bulbous, *hollow, often very conspicuous horns*. Androecia on short lateral or long leafy branches, often proliferating distally; bracts imbricate, forming a sharply defined spike, each more or less equally bifid, inflated, usually in 3–8, rarely up to 12 pairs; *bracteole present only at base of spike*, smaller than normal underleaf. Capsule and elaters as described under *C. cubensis*. Spores large, chlorophyllose, usually becoming pluricellular within the capsule (precocious germination), finely verruculose with a superimposed pattern of coarse papillae oriented to form rosettes.

GENOTYPE: *Jungermannia cornuta* Lindenb. (= *C. cornuta* (Lindenb.) Steph.), a species widespread in tropical America, from Cuba to Jamaica (*type*) to Brazil.

Ceratolejeunea is a large and distinctive genus, primarily confined to the New World Tropics, where it is most copiously represented at lower elevations in the mountains. Stephani (1913, p. 391) has listed 100 species, three-fourths (76) of which are from the New World tropics; he added (1923, p. 399) two additional species. Since that time almost a dozen additional species have been published, of which about half were from the New World tropics. Evans (1905, 1907) gave a clear and lucid account of the general features of the genus, sharply defining it from related elements; he confined himself to the Puerto Rican species. More recently, Fulford (1945) has published a brief revision of 19 of the neotropical species, treating the three regional species. Although a number of Stephani species are synonymized, unfortunately the majority of described species from the Americas are not treated in this paper. The relatively few African and Insular Pacific species are poorly known.

As Evans (1905, p. 273) has emphasized, "*Ceratolejeunea* is one of the most natural genera of the Lejeuneaceae." The genus clearly belongs to the Schizostipae, since it shows seven rows of large cortical cells (two of which serve to form the ventral merophytes, giving rise to the underleaves). However, it includes two species with entire underleaves (*C. portoricensis*, *C. deciscens*). This, together with the usually robust size, the brownish pigmentation, and the glossiness, suggests certain genera of Holostipae, particularly *Neurolejeunea* and *Odontolejeunea*. Indeed, the position of the holostipous *C. portoricensis* has been much debated. Evans (1907, pp. 15, 17) placed this species in *Ceratolejeunea*, and is followed in this by Fulford (1945, p. 399). Herzog (1933, pp. 47–48) deals with the position of this species, while Zwickel (1932) arbitrarily places the species in the Holostipae, stating that "alle holostipen *Ceratolejeuneen* von mir nicht als zu *Ceratolejeunea* gehörig betrachtet werden." He would place *C. portoricensis* in the Holostipae, in *Neurolejeunea*. Evans, however, has emphasized that the one-celled apical lobular tooth, with the hyaline papilla at its proximal base, clearly places this species in *Ceratolejeunea*. Fulford (1945, p. 402) does not attempt to decide the position of the holostipous species of *Ceratolejeunea*, merely stating that study of more complete series of species is necessary to determine developmental trends within the genus.

Recently, the writer (Schuster, 1954) has pointed out a sharp and apparently final means of differentiating between these two genera. In *Neurolejeunea* the stem is formed of a large number of cells (*ca.* 15–16 rows of cortical cells), the ventral merophytes, as in other Holostipae, are at least four cells broad. It was pointed out that *Ceratolejeunea*, by contrast, shows the normal seven rows of cortical cells of the Schizostipae, with the ventral merophytes only two cells broad. Since recent examination of *C. portoricensis* and *deciscens* has shown that these species have ventral merophytes formed by two rows of large cortical cells, and have the lobular apices (with one-celled apical teeth, and a proximal hyaline papilla) of typical *Ceratolejeunea*, there appears to be no doubt about the incorrectness of Zwickel's attempt to place them in *Neurolejeunea*. The writer suggests that they be considered deviant members of *Ceratolejeunea*, following thus the carefully reasoned position of Evans (1905).

However, with recent trends towards establishment of smaller and more homogeneous taxa, it seems desirable to separate these extreme species from *Ceratolejeunea* s. str. as a separate subgenus, which may be established as per the following key:

KEY TO SUBGENERA OF CERATOLEJEUNEA

1. Underleaves uniformly bilobed, usually to approximately their middle; bracteoles bifid..... Subgenus *Ceratolejeunea*
1. Underleaves uniformly entire; bracteole entire or retuse.
Subgenus *Ceratophora* subgenus nova[2]

[2] Plantae rufo-brunneae; folia caulina contigua vel parum imbricata; ocelli basales majores, 1–2; amphigastria caulina subrotunda, integerrima; amphigastrium florale magnum, integerrimum.

TYPE: *C. deciscens* (Sande Lacoste) Steph. *C. portoricensis* (Hampe et G.) Evs. also appears to belong in this subgenus, although only remotely allied to *C. deciscens*.

All our species belong to the subgenus *Ceratolejeunea*, i.e., they are clearly schizostipous; their separation from the single local species of the holostipous *Neurolejeunea* offers no problem.

The regional species of *Ceratolejeunea* are among the less specialized representatives of the genus. They fail to show, or show to only a slight degree, two of the most striking peculiarities of the genus: sharply horned perianths, and "utriculi." As emphasized in the classical paper of Evans, the "perianth is perhaps the most striking feature of the genus." The four keels (the antical is normally suppressed) grow out into distinct horns, which may be long and tubular, or strongly bulbous. Our regional species vary from virtually unhorned (*C. laeta-fusca*), with merely four roughened keels that do not clearly extend beyond the beak, to obtusely and weakly "horned", with horns extending to a slight degree beyond the beak (*C. rubiginosa*, *C. cubensis*). Even in the latter case, the degree of development of the horns merely foreshadows the extremes attained by some of the tropical species.

The second peculiarity of the genus is represented by the modified leaf (or pair of leaves), found at the bases of some branches. In these leaves the lobule is vastly increased in size, strongly gibbous and inflated, forming a large water-sac. In the regional species with the least specialized perianths, such water-sacs do not occur, but they are occasionally found in *C. cubensis* (although I have not seen them in regional plants).

Ceratolejeunea is separable from other regional Lejeuneaceae by the warm, reddish- to golden-brownish color, the glossiness of dry plants, and the closely prostrate growth. It superficially resembles regional members of such holostipous genera as *Lopholejeunea* and *Neurolejeunea*, but differs from these in three important features: (1) the bilobed underleaves; (2) the presence of a basal group of ocelli; (3) the coarsely segmented oil-bodies. The color of our regional *Ceratolejeunea* species is also a much paler or warmer brown, *Lopholejeunea* and *Neurolejeunea* being a distinct fuscous-brown to blackish in color. This feature alone suffices to separate our *Ceratolejeuneae*.

The genus is not at all closely related to any other genus of the Schizostipae. The secondary pigmentation, the four-keeled and generally horned perianths, and frequently dentate leaf-lobes at once separate *Ceratolejeunea* from our other genera of Schizostipae. Particularly distinctive are the cellular features (recently emphasized by Schuster and Hattori, 1954). Most (and all of our) species show a group of basal ocelli, rarely a single basal ocellus. The leaf-cells either have large radiate trigones and intermediate thickenings (with limited thin places), resulting in walls that appear to be more or less sinuously thickened, or else the radiate trigones and the intermediate thickenings are almost coalescent (leaving only narrow and sharply defined pits between them), resulting in superficially strongly and equally thickened cell walls. In either case the middle lamella is much more strongly brownish pigmented than the rest of the cell-walls. This feature is extremely distinctive of all species of the genus. The vegetative cells, in all studied species, show several (4–5 usually) relatively small and coarsely segmented oil-bodies. As pointed out previously (Schuster, 1954), the oil-bodies

of the studied species of *Ceratolejeunea* are very different from those of *Neurolejeunea breutelii*.

Of our three species, two occur sporadically and apparently rarely in the tropical area south of Miami, Fla. The third species is more widespread, occurring (somewhat like the subtropical epiphytic orchid, *Epidendrum conopseum*) along the immediate Gulf Coastal Plain from Florida to Louisiana, and northward along the Atlantic coast to South Carolina.

KEY TO SPECIES

1. Apices of leaves quite entire, more or less rounded; perianths with the four keels scarcely produced as distinct horns: at most as obtuse crests, extended barely beyond beak of perianth; bases of leaves with 1–3 (4) ocelli, not vittate; utriculi absent; dioecious. Widespread..... *C. laete-fusca*
1. Apices of leaves (at least on some mature leaves), sparingly dentate to serrate; perianths with distinct knob-like or conical horns, extended beyond beak of perianth; autoecious. Very local.....2.
2. Ocelli in a group of 2(3–4) at base of lobe; dorsal lobes usually obscurely repand-dentate at apices, on many leaves entire; sometimes with utriculi; plants yellowish-brown. *C. cubensis*
2. Ocelli in a short vitta 2-3 or up to 4–5 cells long; dorsal lobes, particularly anterior margin, sometimes distinctly serrate-dentate; without utriculi; plants reddish-brown. *C. rubiginosa*

Ceratolejeunea rubiginosa Steph.

Lejeunea cubensis Gottsche, *in Hep. Cubensis Wrightianae*; *non* Montagne.
Ceratolejeunea rubiginosa Stephani, Hedwigia **34:** 237, 1895; Fulford, Brittonia **5:** 397, figs. 96–106, 1945; Frye and Clark, Univ. Wash. Publ. Biol. **6**(5): 852, 1947.
Ceratolejeunea pseudoneura Zwickel, Ann. Bryol. **6:** 110, fig. 1, a–k, 1933.

In loose, prostrate mats, *reddish-brown*, *nitid*, rather small (averaging *750–850 μ wide*, *rarely up to 1000–1500 μ wide* × 8–20 mm. long), rather freely but irregularly pinnately branched; branches sometimes somewhat microphyllous (but without sharp distinction between "normal" and microphyllous types). Stems 65–75 μ (95–100 μ) in diam., deep reddish-brown; ventral cortical cells *ca.* 23–28 (32–38) μ wide × 36–42 (48) μ long, thick-walled. Leaves slightly to moderately imbricate, slightly convex, spreading to falcate (65–85° angle with stem; the posterior margin of free dorsal lobe often at an angle of 80–100°, weakly arched to nearly straight); dorsal lobe obliquely ovate or falcate-ovate, asymmetric, 400–600 μ long × 300–360 (400) μ wide, *averaging 3–4 × length of lobule*; dorsal margin strongly arcuate from a nearly straight basal portion, the narrowed apex rounded *to obscurely apiculate, frequently with a few obscure teeth of the antical, subapical margin*; posterior margin usually nearly straight, edentate. Lobule *relatively small* (116–125 μ long in smaller phases, up to 145 μ long in larger phases), obliquely ovate, strongly inflated, slightly constricted just below opening, the *apical tooth relatively short* (14–20 μ long) *and blunt or subacute, weakly or not curved*; hyaline papilla often large and clavate (up to 6 × 24 μ), attached to proximal base of apical tooth; *utriculi not developed*.[3] Cells of the apex, along the margins, 11–12.5 μ, *the subapical intramarginal cells ca. 18 μ*, the sub-basal and basal cells 18–23 × 18–25 μ; cell-walls more or less evenly thickened, the trigones small, or with strong triradiate and intermediate thickenings (sometimes confluent), the sub-basal cells becoming markedly thick-walled; middle lamella not deeply pigmented; ocelli in mature plants *in a single row of 2–4, occasionally 5–6* (sometimes, on robust leaves, with a partial second row), but very *often the majority of leaves with 1 ocellus, or only a row of 2*; ocelli from 23 × 36 μ

[3] Not observed by either Fulford (1945) or myself, but reported as present by Zwickel (1933).

to 25 × 40–45 μ, rarely up to 34 × 54 μ. Underleaves distant, suborbicular to broadly ovate, rather small, 2–3 × width of stem (150–180 μ long and 145–190 μ wide on smaller phases; up to 350 μ long and wide on robust extremes), bilobed *ca.* ½ their total length (⅔–¾ to the rounded rhizoid-initial disk), the lobes acute, 6–7 or more cells broad at base, erect to erect-spreading, entire-margined. Without asexual reproduction.

Autoecious. Androecia usually as short, determinate, lateral spikes on branches with 0–2 pairs of vegetative leaves, more rarely terminal on leading shoots; androecium *ca.* 340–380 (425) μ wide, compactly spicate; bracts closely imbricate, in 3–8 pairs usually (rarely in 2 pairs); bracts up to 240 μ long with lobule up to 175 μ long, gibbous, the outer portion of keel between lobe and lobule often crenulate with elevated cells; diandrous; bracteole at base on androecium (sometimes, on longer androecia, 2 bracteoles), similar to underleaves but usually more ovate, often with more divergent lobes. Female inflorescence most often on short, nearly leafless lateral branches, *producing a single innovation*. Bracts obliquely spreading or erect-spreading; lobe subequal to leaves in size, polymorphic, usually obovate from a slender base, varying from subentire to rather coarsely but sparsely dentate and rounded to acute to suddenly acuminate at apex, *ca.* (450) 550–700 μ long × (270) 330–400 μ wide; lobule *narrow*, 100–130 (140) μ wide × (260) 300–450 μ long, free for half or more of its length, lanceolate to lingulate, acuminate to bidentate at apex (one tooth usually much smaller than the other), the teeth often sharp and acuminate. Bracteole oval, *ca.* 230–260 μ wide × (330) 360–380 μ long, bifid to one-third of its length or to the middle, the lobes acute to subacuminate, entire. Perianth (370) 380–400 (425) × 560–800 μ long, exserted up to half its length, exclusive of horns widest near middle, *the four horns distinct, triangular, slightly compressed, rather short, obtuse to subacute*, occasionally acute, considerably exceeding the short and rather broad, recessed beak; cells of perianth (exclusive of horns) exceedingly strongly, evenly thick-walled (with middle lamella sharply defined), *strongly convex and gibbous*, the keels below the horns consequently appearing distinctly crenulate in profile; median perianth cells *ca.* 23–24 (28) μ wide × 30–35 μ long.

TYPE: Cuba (*Hepaticae Cubensis Wrightianae*, coll. Wright).

DISTRIBUTION.—A rare and apparently rather local species, found at a number of localities in Cuba (Banao Hills; Caraensey Valley; Sierra Maestra; near Herradura; Trinidad Mountain; La Prenda, Guatanamo), and sparingly in a small area in the edge of the "Everglades Keys" of Florida. Although especially searched for during the last six years, it has been wholly impossible to relocate in our area. It may now be extinct in Florida.

Florida: DADE CO. (Between Cutler and Camp Longview, n. of Homestead, *Small and Carter 1431!* NYBG; admixed with *C. cubensis*; near Camp Longview, *Small and Wilson 1527!* NYBG; admixed with *C. cubensis*).

ECOLOGY.—At least in our area corticolous, in deep, tropical "hammock" forests, on the lower portions of the trunks of trees. In the first of the two cited collections, *Trichomanes*, a filmy fern, is admixed; in both collections there is free admixture with *C. cubensis*, a very closely allied species.

DIFFERENTIATION.—Originally confused with *C. cubensis*, the species is often hardly separable from it. Although the species may become relatively robust in Cuba (up to 1–1.5 mm. wide), the local material is of a more slender phase, rarely exceeding 750–850 μ in width. Such plants agree closely with regional material of *C. cubensis* in size. This variation appears to have induced Fulford to describe it (1945, p. 397) as "small" but then to stress as one of the "distinguishing characteristics" its "large size."

The plants share with *C. cubensis* an essentially similar type of perianth: this

is armed with four horns that are triangular in profile, and are in most cases somewhat compressed, as Zwickel (1933, p. 111) correctly noted, describing them as "brevissimus, complanatis." This scarcely agrees with the description of the horns by Fulford (1945, p. 397) as "broad, inflated, appearing as knobs." The figures given by Fulford and Zwickel, however, agree (they were based on the same plants, from *Hep. Cub. Wright.*). The Florida plants (which were first identified with *C. rubiginosa* by Fulford), however, have somewhat longer horns, extending considerably beyond the apex of the beak; typically, they are also considerably more acute. In this they closely approach the commoner phases of *C. cubensis*.

The tendency for the distal portions of the dorsal lobes to be obscurely repand-dentate or subserrate is equally inconstantly developed in *C. rubiginosa* and *C. cubensis*. However, some plants can always be found with vaguely indicated dentition, and obtusely pointed or acute lobes. Such lobes are never produced in *C. laete-fusca* and *C. guianensis*, which are otherwise very similar. The tendency to develop marginal serration is more highly expressed in the robust type material than in the somewhat impoverished (yet freely fertile) Floridian plants. The latter, therefore, are to be separated from *C. laete-fusca* with great care.

Ceratolejeunea rubiginosa differs from both *C. cubensis* and *C. laete-fusca* in one important respect: the orientation of the ocelli. In the latter two species there are 1–3 ocelli usually present; when more than one, the ocelli are equidistant from the leaf-base, either side by side, or separated by one (rarely several) vegetative cell. Under no condition are they ever in a row. By contrast, *C. rubiginosa* has the ocelli in a distinct basal vitta. In well-developed plants (type) they are often 5–6 in a row, occasionally with a few in a partial second approximated row, and may extend to the leaf-middle. The Floridian plants, however, show often merely two ocelli in a row (or separated by a "normal" cell), much less frequently three, rarely four in a row; there is virtually never a trace of a second row. In many plants only a single ocellus is found in most lobes, and such plants are to be separated from our other two species with great care. However, there are nearly always some leaves with a short or interrupted vitta of ocelli, whose presence is absolutely diagnostic. *C. rubiginosa* also differs from *C. cubensis* in having a somewhat more reddish-brown color and very slightly larger leaf-cells.

The Floridian plants studied (*Small and Carter 1431*) are freely fertile, bearing capsules and androecia. The perianths, at least of the plants of this collection, are extremely variable, showing a latitude of variation greater than indicated for the species by Fulford (1945).[4] The variability is almost wholly in regard to the size, number, and orientation of the horns of the perianth. Typically, in *C. rubiginosa*, we find four horns, as in the other species of the genus. The two lateral and two postical horns are usually equally sharp, and virtually

[4] The Floridian plants are also somewhat more slender than the typical plants from Cuba. The minimal measurements, usually given in parentheses, in the description are derived from these plants.

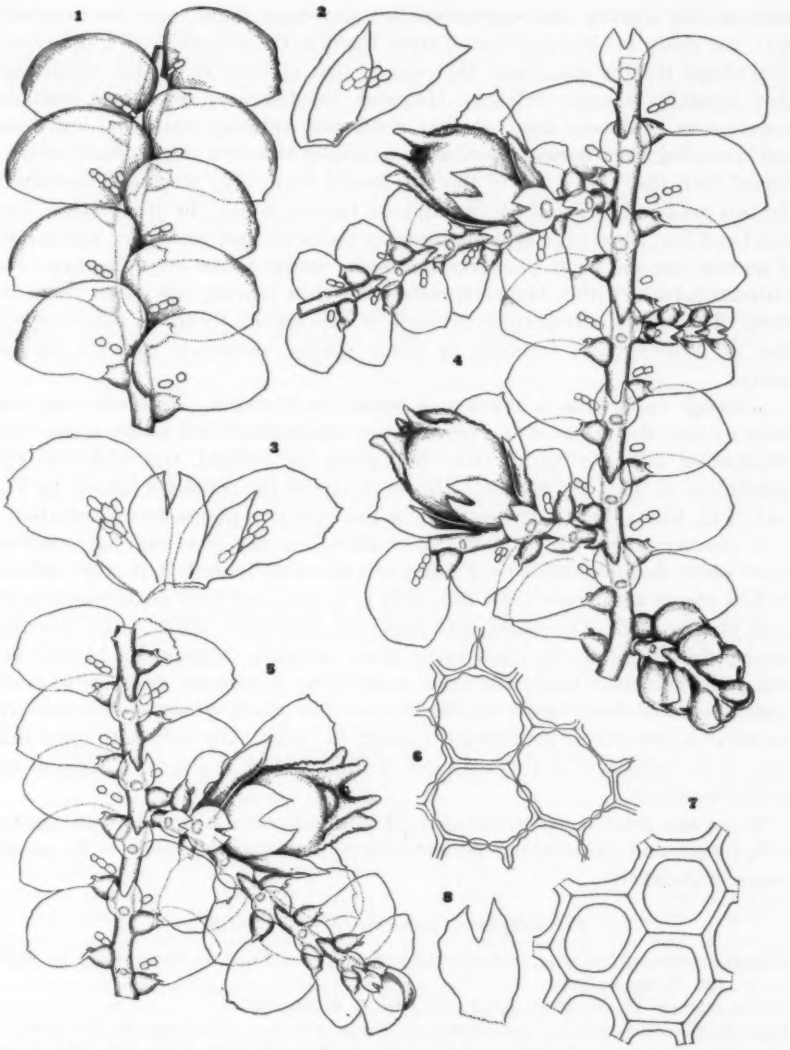

FIG. XX. *Ceratolejeunea rubiginosa* Steph. 1. Antical view of sector of sterile shoot, with maximal development of ocelli (× 44); 2. Female bract (× 50); 3. Female bracts and bracteole, the ocelli drawn in (× 50); 4. Fertile plant, postical aspect, with atypical perianths, the upper 3-horned, the lower 4-horned, but with one horn antical in position (× 40); 5. Shoot-sector, with "normal" perianth (× 40); 6. Median leaf cells (× 500); 7. Median cells of perianth (× 418); 8. Bracteole (× 50). (All figures from *Small and Carter 1431*, Florida).

erect or only slightly erect-spreading. In many cases these horns are as prominent and sharp as, or somewhat sharper than, in *C. cubensis*, and appear more compressed than is commonly the case in that species (in neither species are they normally strongly inflated). However, the following deviations from the norm occur: (1) lateral horns sharply developed, although somewhat less acute and spreading than normal; *postical horns wholly absent*; a single, small, antero-lateral horn just above one of the two lateral horns; (2) perianth five-horned, the two postical horns and one lateral horn normal in size, the other lateral horn small and low, blunt; the antical, normally vestigial, keel grown out into a horn of normal size and form; (3) perianth wholly similar to the preceding type, but with antical keel with a blunt, obsolete horn, thus bearing only three "normal" horns. The highly polymorphic perianth of this species recalls in some respects that of *Neurolejeunea breutelii*, in which similar variability in horn number occurs.

Although variable as to number of horns, the Floridian plants are quite uniform in that the horns of the perianth are compressed and rather acute, thus disagreeing with the figures (103, 106) given by Fulford, and with Fulford's description of them as "stubby." However, one of the perianths figured by Fulford (Fig. 105) closely matches those of the Floridian plants here illustrated.

As already noted, the regional plants differ from the type material in having fewer ocelli than indicated by Fulford and Zwickel. Indeed, it is often difficult to find plants with more than 2–3 ocelli in a row, and very often leaves occur with single ocelli. Associated with this, the Floridian plants have subentire leaves, the apices of the lobes being often rounded, occasionally bluntly and obscurely apiculate (with the apex marked by a solitary cell), occasionally slightly sinuous-denticulate. In this respect the plants disagree with the type material, as illustrated by Fulford. Indeed, the plants key only with great difficulty to *C. rubiginosa* in Fulford's key, tending to key to either "*C. guianensis*" or *C. brevinervis*.

As already pointed out by Zwickel (1933), *C. brevinervis* is a dioecious species, with longer and more salient perianth-horns than *C. rubiginosa* (= *C. pseudoneura* of Zwickel).

Ceratolejeunea cubensis (Mont.) Schiffn.

Lejeunea cubensis Montagne, *in* Ramon de la Sagra, Hist. Fis. Pol. Natur. Cuba II, **9:** 287, pl. 18, fig. 2, 1845.

Colura cubensis Trevis. Mem. Ist. Lomb., Ser. 3, **4:** 402, 1877.

Lejeunea (Cerato-Lejeunea) cubensis Spruce, Trans. Bot. Soc. Edinburgh **15:** 202, 1884.

Ceratolejeunea cubensis Schiffn., *in* Engler-Prantl, Nat. Pfl.-Fam. **1** (3): 125, 1893; Evans, Bull. Torrey Bot. Club **32:** 189, 1905; Fulford, Brittonia **5:** 396, figs. 107–114, 1945; Schuster and Hattori, Jour. Hattori Bot. Lab. No. 11: 32, pl. 6, figs. 4, 4a, 1954.

Ceratolejeunea mosenii Steph., Spec. Hep. **5:** 428, 1913.

Plants small to medium-sized, in prostrate, *reddish-brown or light, yellowish-brown patches* (rarely somewhat greenish); *shoots 750–1200 μ wide* (rarely up to 1400 μ × 1–3 cm. long), sparingly to frequently, irregularly pinnately branched. Stems brownish, usually (70) 90–110 μ in diam.; ventral cortical cells large, (24) 30–37 μ wide × 35–52 μ long. Leaves contiguous to weakly imbricate, somewhat convex, the leaf-apices usually deflexed (both

when dry and moist); lobes somewhat convex, spreading at an angle of 75–90° (the nearly straight posterior margin at 80–100°), *asymmetrically ovate, somewhat falcate, ca.* 450 μ long × 350 μ wide to 560 μ long × 430–500 μ wide, *averaging 3.5–4.5 × length of lobule*, dorsal margin strongly arcuate, the lobe narrowed to a *somewhat pointed, usually sparingly repand-serrulate apical region* (the denticulations often 1-celled, usually only 2–3 per mature leaf; weak shoots often with margins quite entire). Lobule very strongly inflated, *relatively small* (up to 120–160 μ long, rarely up to 180 μ), ovate, slightly constricted before the oblique, slightly flaring, circular mouth, the free margin involute to the apical tooth; apical tooth rather *large, up to 26–29 μ long, usually strongly hooked and pointed*, often falcate and gradually attenuate; hyaline papilla prominent, at proximal base of apical tooth. Large utriculi occasionally developed (not observed in regional material). Cells of the apex, along the margins, 11–13 μ; cells of apical, intramarginal region *16–17* (*18*) μ; cells near base, in ocellar region, *16–18 × 20–27* μ; cell-walls more or less evenly thick-walled, varying from slightly thick-walled to strongly so (then with distinct pits), the walls brownish, the *middle lamella conspicuously darker*; *ocelli large, 23–26 μ × 36–44* (*occasionally 46–48*) μ, *typically 2 or 3* (*4*) *in a transverse group* (often one separated from the others by a vegetative cell), *never seriate*; oil-body of ocellus large, homogeneous and glistening (with death, breaking up into spherical segments), *ca. 20–21 × 38–39*, up to 22 × 45 μ; oil-bodies of vegetative cells 3–3.6 to 3 × 6–8 μ, occasionally a few up to 3 × 10–13 μ, 2–4 per cell, sharply segmented, usually of 2 rows of (4–15) segments, each *ca.* 1–1.5 μ. Underleaves *rotund*, rather small and distant, 160–200 (up to 225–280) μ wide and long, the triangular, acute to blunt, suberect to erect lobes 5–6(7–9) cells wide at base, the sinus descending to middle (⅗ the length to rhizoid-initial field). Without asexual reproduction, the leaves persistent (but frequently with regenerations from persistent leaves).

Autoecious. Androecia usually lateral compact spikes, *ca.* 350 μ wide, often constituting the whole branch, more occasionally terminal on long, leafy branches; bracts in 2–10 pairs; with 1 (rarely 2) basal bracteole. Female bracts obliquely spreading, the lobe similar to leaf-lobe (but with margin usually more coarsely dentate or serrate), the lobule narrowly ovate to lanceolate, smaller than lobe, the free portion triangularly narrowed, often faintly few-toothed; lobule free for half or less of its length. Bracteole ovate, bifid *ca.* ⅓ of its length, the lobes erect and acute, nearly or quite entire-margined. Perianth obovoid, emergent for half or more of its length (with maturation of sporophyte often somewhat stipitate from a fleshy base and then long-exserted), 320–360 μ wide × 600 μ long or more, up to 600 × 900 μ, the apex somewhat narrowed to the 4 erect, *usually acute to subacute* (rarely knob-like) *horns, the horns rather short*, but far exceeding the short and inconspicuous, recessed, beak; cells of perianth-surface, below horns, thick-walled, with obvious middle-lamella, gibbous, the surface appearing roughened; median cells of perianth *ca.* 23–25 × 30–35 μ. Sporophyte rather shortly pedicellate, the seta *ca.* 180 μ in diam., formed of 4 interior, 12 epidermal cell-rows, the cells evenly and quite distinctly thick-walled. Capsule whitish when empty, the thickenings of the cell-wall essentially unpigmented; valves *ca.* 180 μ wide × 300 μ long. Epidermal cells *without localized thickenings*, the radial walls somewhat thickened at their intersections; marginal 2 cell-rows of each valve small and subquadrate to rectangulate, averaging (16) 18–20 μ long × 11–14 (16) μ wide, the cells within the 2 marginal rows of the valves suddenly larger, irregular in shape, *ca.* 20–25 × 40–52 μ. Inner cells much more delicate, rather irregular except near the tips of the valves (where *ca.* 18–24 μ and subquadrate or short-rectangulate), with pellucid but well-defined, *rather coarse nodular thickenings* (which are often dilated at their rounded outer ends), usually 1–2 (3–4) per wall.

TYPE: Cuba (Ramon de la Sagra) in the Montagne Herbarium (a fragment, from the Mitten Herbarium, at the NYBG!).

DISTRIBUTION.—A tropical species ranging from the Amazonian Region (from Para to the Rio Negros and probably widespread elsewhere) of Brazil to Panama, Guatemala, British Honduras, and the West Indies (Jamaica!, Bahamas!,

Cuba!, *type*!; Isle of Pines!); local and rather rare in our region, where it is limited evidently almost wholly to the Everglade Keys region, from Miami westward and southward. As in the case of many of the species of the dense hammocks once widespread in this area, intensive real estate operations and fires have almost wiped out the species in our area.

Florida: DADE CO. (Nixon-Lewis Hammock; Goodburn Hammock; Timms Hammock; Royal Palm State Park [Paradise Key]; hammocks near the Homestead Trail, near Silver Palm School; Horton Hammock; between Cutler and Camp Longview; near Camp Longview in hammocks near the Homestead Trail, *Small and Carter 1355 pp., 1431*; *Small and Wilson 1527*; *Small et al. 1527!, 7010!, 1431!, 2349!, 5232!, 5244!, 5291!*; *Britton and Britton 561!*; Sykes Hammock, *Small, Mosier and Small 5259*. All these collections predate 1920; the only recent collections are those from Timms Hammock, on Bauer Drive, near Modello, *RMS 22915, 22857*, 1951; Costello Hammock, near Silver Palm, *RMS 22964*; Mahogany-Royal Palm Hammock s.w. of tip of Long Key Pineland, Everglades, *RMS 37301, 37306a, 37308*).

ECOLOGY.—Regionally exclusively a "hammock" species, limited to the humid and dense islands of tropical evergreen trees and almost restricted to the limited limestone "islands" lying west and south of Miami. In our area almost exclusively on bark, often with filmy ferns (*Trichomanis krausii*) and with various Hepaticae (*Radula australis*, *Plagiochila ludoviciana* and *hypnoides*, *Lopholejeunea sagreana*, *Ceratolejeunea rubiginosa*, *Cheilolejeunea decidua*, *clausa*, and *rigidula*, etc.), forming large, olive-brown to yellowish-brown, glistening mats. The species is not a pioneer, more often coming in after preparation by other species such as *Caudalejeunea* or *Plagiochila hypnoides*; it may actually be epiphytic on the latter. More rarely on decaying logs, there sometimes with *Cheilolejeunea decidua*. In the tropical area to our south often on rocks or on living leaves.

Although almost all collections seen are from the limited region of the Everglades Keys, the best development of the species that has been seen is from a large hammock just southwest of the tip of Long Key Pineland ("Long Pine Key"), in western Dade County, lying some 2.5 miles west of the southwest bend in the Ingraham Highway (Cape Sable Road). The species occurs here in a large hammock, whose mature vegetation is dominated by very large trees of *Swietenia mahogani* (West Indian Mahogany), with *Quercus virginiana*, *Ocotea catesbyana*, *Ficus aurea*, *Chrysophyllum olivaeforme*, *Roystonea regia*, *Sabal palmetto* as accessory trees, with the hammock-margin with dense stands of the rare palm *Paurotis wrightii*. This almost inaccessible hammock, wholly surrounded by sloughs and sawgrass, has in the center a small colony of Royal Palms, at the bases of which the *Ceratolejeunea* occurs. The species here is well developed and bears both androecia and capsules. Associated are *Lejeunea* (*Microlejeunea*) *laetevirens*, *L. bullata*, *L. flava*, *Rectolejeunea berteroana*, *R. brittoniae*, *Diplasiolejeunea rudolphiana*, *Cololejeunea subcristata*, *Caudalejeunea lehmanniana*, *Leptolejeunea elliptica*, *Cheilolejeunea rigidula*, *Leptocolea cardiocarpa*, *Radula australis* and *Plagiochila hypnoides*.

DIFFERENTIATION.—Superficially almost indistinguishable from our other two

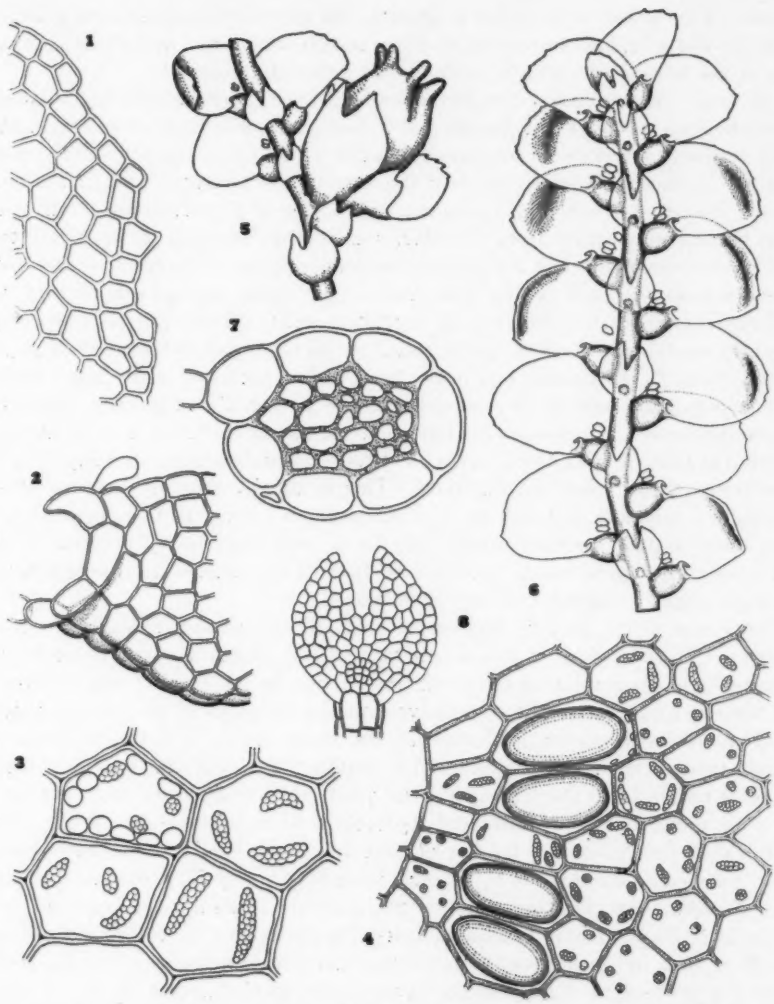

FIG. XXI. *Ceratolejeunea cubensis* (Mont.) Schiffn. 1. Apex of leaf lobe (× 468); 2. Apex of lobule, showing hyaline papilla (× 325); 3. Median cells with oil-bodies; in upper left cell, chloroplasts (× 925); 4. Basal cells, with ocelli and oil-bodies drawn in, the leaf base at left (× 375); 5. Perianth-bearing shoot-sector (× *ca.* 32); 6. Sterile shoot, postical view (× 50); 7. Stem cross-section (× 320); 8. Mature underleaf, showing insertion on stem (× 135). (Figs. 1–4, Timms Hammock, Dade Co., Florida, *Schuster*, 1951; 5, after Fulford, 1945; 6–8, Costello Hammock, Dade Co., Florida, *Schuster 22964*).

species of the genus, with which it agrees in the general size, decumbent growth, olive-brown to golden-brown color, shiny texture when dry, and slight convexity of the leaves, which have more or less deflexed apices.

In many respects, including frequency, the species stands midway between our other two species, *C. rubiginosa* and *C. laete-fusca*. The more or less apiculate and remotely serrulate or irregularly dentate lobe apices, the apparently constantly autoecious inflorescence, and the form of the perianth (with four rather short, spreading to suberect, triangular horns) suggest *C. rubiginosa*. *C. cubensis* can be told most easily from *C. rubiginosa* by the following features: (1) the ocelli are never more than 2–3 (4) per leaf base, and are oriented in an arc equidistant from the base of the lobe; they occur either juxtaposed, or may be separated from each other by 1–2 vegetative cells; (2) the leaf-cells are very slightly smaller, their width in the apical region averaging perhaps 16–17 μ (*vs.* 18 or 19 μ in *C. rubiginosa*), and in the basal region, exclusive of the larger ocelli, the cells average only 16–18 μ in width (*vs.* 18–23 μ in *C. rubiginosa*). Although these differences in cell-size are slight, careful measurement of a series of cell-rows will always bring them out. *C. cubensis* also differs from *C. rubiginosa* in the form of the apical lobular tooth. This is usually strongly hooked, often strongly acuminate, and may be as much as 26–28 μ long. In *C. rubiginosa* it is less often sharply hooked, stouter, (14–19 μ), and less sharply pointed. In *C. laete-fusca* the apical tooth is similar to that of *C. rubiginosa*, although occasionally slightly sharper and better developed.

As Evans (1911, p. 215) has emphasized, the present species and *C. laete-fusca* (= *C. integrifolia* of Evans) are very closely allied. The two agree in the number and orientation of the ocelli, in cell size, in the form of the cell-walls, in the size and form of the underleaves, and in the form of the lobules, bracts and bracteoles. However, in *C. cubensis* the leaves (or those of the branches, at least) tend to be weakly dentate, with usually 2–5 apical and subapical teeth (one of which forms the lobe-apex), the bracts tend to have the lobes similarly or even more sharply dentate, and the ocelli tend to be somewhat larger. This latter difference is used in the key of Frye and Clark (1947, p. 852) to separate the two species, the ocelli of *C. cubensis* being supposedly 27 $\times$ 45 μ *vs.* 16 $\times$ 35 μ in *C. laete-fusca*. However, in true material of *C. cubensis* the ocelli may be only 23 $\times$ 36 μ, while in typical *C. laete-fusca* the ocelli may be occasionally up to 25 $\times$ 45 μ, indicating that both species show a wide range in size of the ocelli. There is probably a slightly greater average size in *C. cubensis*.

As Schuster and Hattori (1954) have pointed out, there is little difference in the form of the leaf-cells, in their size, or in the oil-bodies, that is at all significant. The cells of *C. cubensis* are, admittedly, very slightly larger, although the differences are so slight that they have more theoretical than practical significance. When fertile, the horned perianths of *C. cubensis* (similar to those of *C. rubiginosa*) at once separate the species from *C. laete-fusca*. *C. cubensis* occasionally produces utriculi; in *C. laete-fusca* they have never been observed.

Perhaps even more closely allied to *C. cubensis* is the recently described *C. lobata* Clark (Proc. Cal. Acad. Sci., 4th Ser., **27** (18): 599, 1953). This species

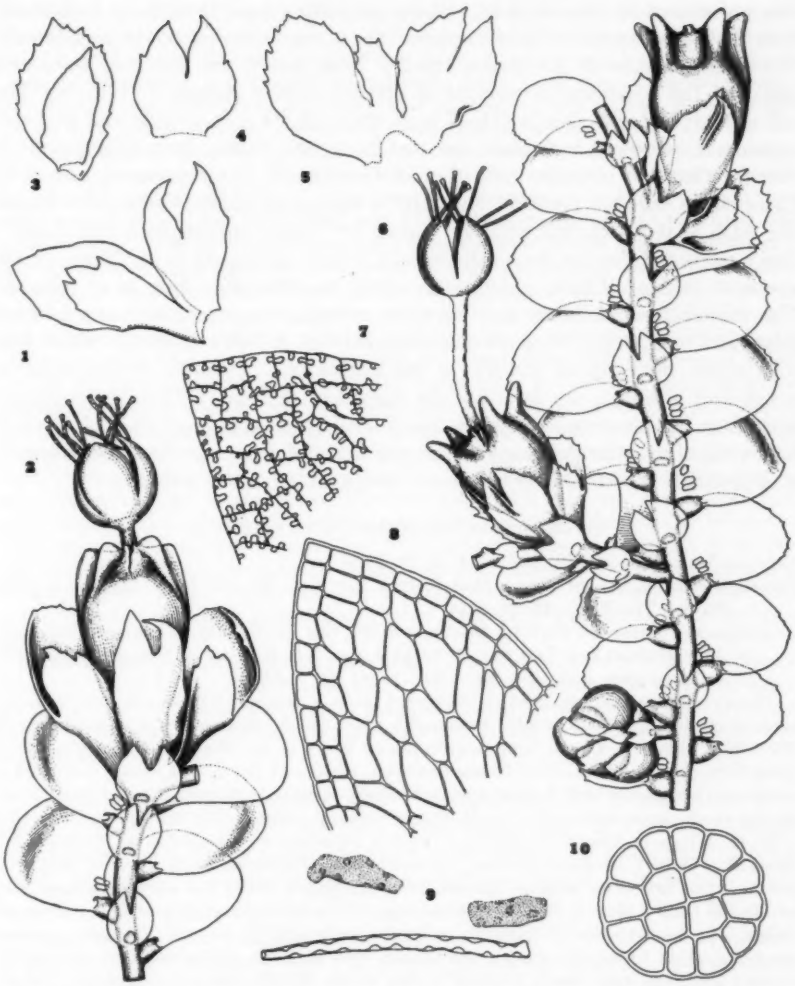

FIG. XXII. *Ceratolejeunea laete-fusca* (Aust.) Schust. 1. Bract and bractole (× 45); 2. Fertile stem, with open capsule, the subfloral innovation cut off at base (× 48). *Ceratolejeunea cubensis* (Mont.) Schiffn. 3–5. Bract, bracteole, and bract united at base to bracteole (× 45); 6. Fertile plant, postical aspect, the subfloral innovations cut off above base (× 42); 7. Inner cell-layer of capsule-wall, apex of valve (× 235); 8. Epidermal cells of capsule-wall (× 235); 9. Two spores and an elater (× 235); 10. Cross-section of seta (× 135). (*C. laete-fusca*, Figs. 1–2, Costello Hammock, Dade Co., Florida, *Schuster 22959*; *C. cubensis*, Figs. 3–10, Mahogany-Royal Palm Hammock, s.w. of Long Key Pineland, Everglades National Park, Florida, *Schuster 37301*).

was unfortunately described as without perianths, even though its author admits that it is therefore "hard to place." On a vegetative basis, the occasionally 2–3-dentate apices of the leaves, the 2–3 basal ocelli, the underleaf form and size, and the occasional occurrence of utricles, closely suggest *C. cubensis*. The cell size given for *C. lobata* (11–17 μ at apex; 20–34 μ in middle and at base) appears to represent individual cell measurements, rather than averages. It is therefore hard to compare with that of *C. cubensis*, but appears to exceed it. Clark states that her plant is "bisexual," a statement which is difficult to reconcile with that which immediately follows it: "male inflorescence not found." One supposed difference lies in the lobules, which are stated to be "large, ovoid, about 14 × 8 μ" (Clark, p. 598) while they are 120–180 μ long in *C. cubensis*. The calculations of Clark are, however, certainly in error, and computation from her Plate 38, fig. 10, gives a measurement of *ca.* 140 μ in length, which falls well within the range of the size of the lobules of *C. cubensis*. It also must be noted that although she describes the distal leaf cells as 11–17 μ, my computations from her illustrations (Pl. 38, figs. 5–7) show an *average* of 10–12.5 μ, which falls virtually within the range of the cell size of *C. cubensis*. As a consequence, it is probable that *C. lobata* will prove inseparable from *C. cubensis*.

Ceratolejeunea laete-fusca (Aust.) comb. n.

Lejeunea laete-fusca Austin, Bot. Gaz. **1:** 36, 1876.

Ceratolejeunea integrifolia Evans, Bull. Torrey Bot. Club **38:** 213, pl. 9, figs. 13–19, 1911; Evans, The Bryol. **14:** 88, 1911.

Ceratolejeunea guianensis Fulford, Brittonia **5:** 391, figs. 82–87, 1945; Schuster and Hattori, Jour. Hattori Bot. Lab. No. 11: 32, pl. 6, figs. 2, 3, 1954 (not of Nees and Montagne, *in* Montagne, Ann. Sci. Nat., Ser. 2, **14:** 335, 1840).

Plants small to medium-sized, in depressed mats, *yellowish-brown to olive-brown* (rarely somewhat olive-greenish), quite translucent when moist, *shiny when dry*; *shoots mostly 780–1100* μ wide × 1–2.5 cm. long, sterile plants freely or sparingly, fertile plants freely, irregularly pinnately branched. Stems brownish, 60–95 μ in diam., not closely attached to substrate; branches widely to obliquely spreading, tending to become parallel in old mats, similar to the stem, *never with utriculi at base*; ventral cortical stem cells 23–28 (30) μ wide × 32–48 (64) μ long. Leaves contiguous to weakly imbricate, somewhat convex. Lobes widely spreading (65–80°), somewhat convex, the apices usually deflexed (both when dry and when moist), ovate and often slightly falcate, 350–400 μ long × 300–370 μ wide, occasionally up to 425–460 (525) μ long × 325–360 (480) μ wide; entire antical margin strongly and evenly arched, the basal portion arching across (and usually slightly beyond) the stem; postical margin straight to weakly convex, continuous with or at an obtuse angle to the slightly arcuate keel, the *apex broad, rounded to very obtuse* (*rarely subacute* on isolated leaves), the *margin quite entire* or vaguely sinuate, slightly crenulate with projecting cells. Lobule strongly inflated, ovate, *ca.* 110–150 μ long, strongly constricted just before the oblique mouth; keel arched and strongly convex; free margins of lobule involute to apical tooth; apical tooth rather short, *ca. 26–30 μ long, usually strongly hooked and sharply pointed*; hyaline papillae at proximal base of apical tooth. *Lobules never modified to form utriculi*. Cells of the leaf-margins, near the apex *very small, 9–11 (12) μ*; *cells of the apical, intramarginal region 13–15 μ*; median cells 14–15 (17) μ wide × 15–19 (21) μ long; basal cells (exclusive of ocelli) 15 × 18–23 μ; *cell-walls appearing nearly uniformly thickened* (the pits indistinct), *with middle-lamellae deep brownish*; *ocelli usually 2–3, side-by-side* (rarely 4, very rarely 5–6 or even 7, equidistant from base, occasionally 1 or 2 separated by vegetative cells), *ca. 16 × 35 μ*, rarely up to 25 × 45–55 μ; vegetative cells with usually 4–5 oil-bodies, ovoid to

bacilliform, *small, usually less than 4 × 6 μ*, composed of at most 2 rows of coarse segments. Underleaves *distant, broadly obovate to orbicular, rounded to the base or broadly cuneate basally*, 160–230 (rarely 250–300) μ wide and long, bilobed for half their length (to ⅔ the distance to the circular, rather small, rhizoid-initial disk); lobes erect, triangular, acute or subobtuse, mostly 6–8 (rarely 9–10) cells wide at base, entire-margined; *underleaf-width 1.5–2.9 (3.1) × the stem width. Without any mode of asexual reproduction.*

Dioecious, most often sterile. Androecia on a short lateral branch, or terminal on long, leafy branches, often proliferating vegetatively; bracts usually in 2–3, rarely 4–6 pairs, *loosely imbricate*, strongly inflated, the arcuate keel roughened with crenulate-protuberant cells, unequally to subequally bilobed, with blunt lobes; usually with a single basal bracteole (rarely 2). Female inflorescences most often on short lateral branches, more infrequently on long, leafy branches, always with a single subfloral innovation; innovations usually long and leafy, sterile. Bracts obliquely spreading, sharply complicate, deeply and quite unequally bilobed, the lobe ovate to obovate, up to 450–600 μ long × 300–350 μ wide (often smaller), polymorphic, rounded to acute at apex, *usually entire* (occasionally with 1–3 weak teeth); lobule *ovate*, relatively large and broad, mostly 350–450 μ long × 180–200 μ wide, the *apical region usually irregularly* 1–3-dentate or 1–3-lobulate; bracteole usually slightly connate on one side, *narrowly oblong to ovate*, to 250 × 500 μ, about half bilobed, with erect to suberect, acute lobes, entire or rarely with 1 (very rarely with 2) teeth per side. Perianth widest near middle (but appearing widest near apex, because of the winged keels), from 320–370 μ wide × 550–600 μ long to a maximum of 450 μ wide × 650 μ long, ⅓–½ emergent, strongly inflated below, the distal half with 2 sharp and high lateral, and 2 nearly equally sharp and high postical keels, which are *weakly produced as compressed, wing-like, angulate shoulders*, extending barely to slightly *beyond the mouth of the short beak*; *shoulders usually rectangulate to slightly acute*, not inflated, the very tips often slightly obtuse; *normally with a fifth, antical keel*, which is much lower, not angularly produced or scarcely so, usually ending some distance below beak and not extending below middle of perianth.[5]

TYPE: Charleston, South Carolina (Sullivant, 1845; *No. 35* in the Austin collections at the NYBG; all of this number was sent by Underwood to Stephani). A second specimen, identified with "*Lejeunea (Cerato-Lej.) laete-fusca* Aust." from Florida (leg. J. Donnell Smith, 1877) by Austin and Stephani, evidently on the basis of comparison with the type, is in the NYBG.[6]

The identity of *L. laete-fusca* with *C. integrifolia* Evs. is clear from these points: (1) the type of *L. laete-fusca* came from north of southern Florida; *C. integrifolia* is the only *Ceratolejeunea* known from north of southern Florida; (2) *L. laete-fusca* is characterized by Austin as: "About the size of *L. flava* (Swartz). Readily distinguished by its fuscous color, and by the 2–3 much enlarged cells in the center next to the basal row." The material was found associated with "*L. ovata* Tayl." (= *Harpalejeunea ovata*) and *L. laete-virens* N.

[5] The angulate shoulders vary considerably in degree of development; frequently they are somewhat erect-spreading, with the upper margins virtually at right angles to the longer axis of the perianth. In such cases, the perianth is almost truncate at the apex, except for the slight, often recessed beak. In other cases, the shoulders are slightly more acutely produced, and somewhat more erect; then the perianth-apex is broadly and crescentically emarginate at the apex, in profile, except for the slight beak.

[6] Correspondence with Dr. Bonner, of the Herb. Boissier, revealed that the type material is no longer in the Stephani collections; it appears to have been lost. For this reason, the collection from Florida, by Donnell Smith, from the Austin herbarium (NYBG), identified with *C. laete-fusca* by Stephani, is here designated as the lectotype. The material is clearly conspecific with *C. integrifolia* Evs.

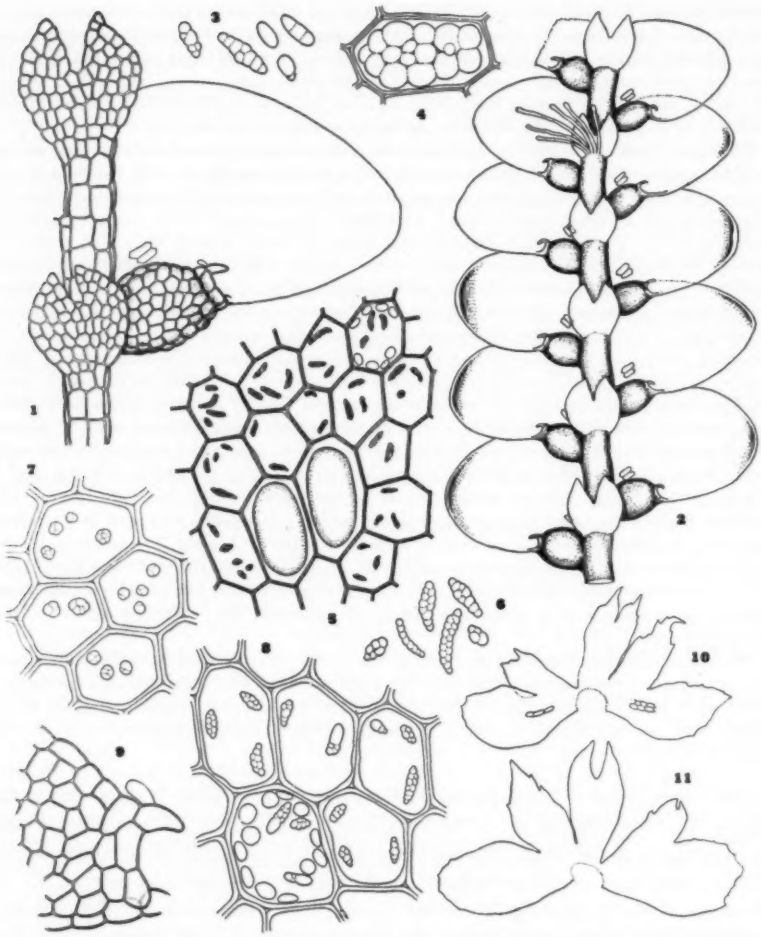

FIG. XXIII. *Ceratolejeunea laete-fusca* (Aust.) Schust. 1. Postical view of shoot-sector (× 135); 2. Sector of sterile shoot, postical view (× 55); 3. Oil-bodies from two adjacent cells (× *ca.* 1450); 4. Ocellus, with oil-body segmented, atypical (× 680); 5. Cells of leaf-base, base below (× 478); 6. Oil-bodies from two adjacent cells (× 1200); 7. Median cells with oil-bodies (× 750); 8. Median cells with oil-bodies; in lower left cell, chloroplasts drawn in (× 680); 9. Apex of lobule (× 275); 10–11. Ring of bracts and bracteole, the ocelli drawn in only in 10 (× 32). (Figs. 1–4, 8–9, Eight miles north of Escatawpa, Miss., *Schuster 19184*; 5–7, Levy Co., Florida, *Schuster F-118*; 10–11, Costello Hammock, Dade Co., Florida, *Schuster 22984*).

and M. From the brief description of Austin, and the emphasis on the color and presence of basal ocelli, only *C. integrifolia* Evs. (= *C. guianensis* Fulford, *nec* Stephani) can be involved.

DISTRIBUTION.—A rather common species of the warmest, most nearly subtropical, portions of the southeastern Coastal Plain. With a distribution closely paralleling that of *Magnolia grandiflora* and *Epidendrum conopseum*, although extending much further southward than these species and not extending quite as far northward along the Atlantic coast. Found throughout peninsular Florida, where it is locally quite abundant, and then in a very narrow, restricted band along the immediate Coastal Plain (inland at most 5–12 miles) northward to South Carolina, westward to Mississippi and Louisiana; i.e., essentially Sabalian in distribution.

South Carolina: CHARLESTON CO. (Charleston, Sullivant, 1845; with *Harpalejeunea ovata* and *Lejeunea laetevirens*; type). It is remarkable that the species has not again been found this far northward in recent times! **Mississippi:** GEORGE CO. (Beech-Magnolia forest, Wyatt Hills, n.e. of Ramsey Springs, *RMS 27691b, 27734, 27720a, 27689b, 27681b, 27681a, 27689*; Wyatt Hills, near Ramsey Springs, 15 mi. e. of Perkinston, *RMS 20179a*); HARRISON CO. (5–7 mi. s. of Ramsey Springs, Schuster, 1953); JACKSON CO. (Swamp along Black Creek, 7–8 mi. n. of Escatawpa, *RMS 27833, 29242a, 29242b, 29242, 29242c, 29248, 29240, 29237, 29255d, 29254c, 27832c, 27832a*; wet swamp, 2–3 mi. n. of Escatawpa, *RMS 27752a*; 6–8 mi. n.e. of VAN CLEAVE, *RMS 19207a, 19230d*; 6–7 mi. n.e. of Van Cleave, west of Pascagoula R., *RMS 27861a, 27791a, 27861b, 27791b, 19211*). **Florida:** No locality data (*J. Donnell Smith, 1877*, NYBG! Lectotype); ALACHUA CO. (Edge of Devils Millhopper, n.w. of Gainesville, *RMS 33480*); CLAY CO. (Ravine of Gold Head Branch State Park, *R. M. and O. M. Schuster 31405a*); DADE CO. (Ross Hammock, n. of Homestead, *RMS 33801a, 33801b*; Costello Hammock, near Silver Palm, n. of Homestead, *RMS 22950, 22959, 22964, c. per.*; Freeman Hammock, Arch Creek Prairie, *Small, Mosier and Small 6148! 6149!*; Shields Hammock, *Small, Mosier and Small 6158, 6155, 6153!*; Murden Hammock, *Small, Mosier and Small 6208!*); DEWAL CO. (*J. Kennedy, 1927*); GADSDEN CO. (Bainbridge Rd. Bridge, *Kurz, 1927*); HERNANDO CO. (Hammock forest 3–4 mi. n.w. of Brooksville, *RMS 22037a, 22111, 22061*); HIGHLANDS CO. (Highlands Hammock State Park, w. of Sebring, *RMS 26004a, 26014, 20108, 19940, 19954d*); HILLSBOROUGH CO. (Hillsborough R. State Park, *RMS 22853, 33940, 33935*); LEVY CO. (Sabal palmetto hammock, just n. of Gulf Hammock, along a canal, *RMS F-118*); LAKE CO. (Hook, 1912); LIBERTY CO. (Alum Bluff, on Appalachicola R., *RMS 33468*; Appalachicola R., *Blomquist 8812!, 8834!*); MARION CO. (Hammock in Juniper Springs, on Rte. 40, in Ocala Ntl. Forest, *RMS 22464, 22467*; in *Taxodium-Nyssa swamp forest* on Oklawaha R., 4 mi. e. of Silver Springs, *RMS 22510a, 22450*; in cypress swamp on Rte. 40, 4 mi. e. of Silver Springs, *RMS 22454a*); POLK CO. (Redfearn, 1952); Seminole Co. (*Rapp 37!*; also issued as "*Ceratolejeunea integrifolia* Evs." *in* Verdoorn's Hep. Select. et Crit. *No. 362*, from Sanford, leg. Rapp! These plants mistakenly labelled as from "loco originalis"); VOLUSIA CO. (Orange City, *Hood 60*). **Louisiana:** No other data ("on *Plagiochila ludoviciana*"; *Drummond*, NYBG!): ST. TAMMANY PARISH. (Covington, *Arsené 14748, 14768, 14394*); TANGIPAHOA PARISH. (One mi. w. of Robert, *Correll 9299!, p. min. p.*; among *Plagiochila ludoviciana, Metzgeria myriapoda, Cheilolejeunea rigidula*).

South of our area known from: **Bahamas:** Soldiers Road, New Providence (*E. G. Britton 882!*); Coppice, Waterloo, New Providence (*E. G. Britton 721*; type of *C. integrifolia* Evs.!). **Cuba:** La Cunagua, Isle of Pines (*Britton, Britton and Wilson 15205!*); Camarioca, Prov. Matanzas (*Britton and Wilson 14025!*); Alto Cedro (*Underwood and Earle 1472! 1549!*); Antilla, Prov. Oriente (*Britton, Britton and Cowell 12514a!*). **Puerto Rico:** Fajardo (*Britton and Shaefer 1724!*).

DISCUSSION.—The species here called *C. laete-fusca* has been variously interpreted. Evans (1902, p. 116) claims that the species is "so incompletely described that we know little about it. . . . Even the type specimens, where accessible, do not aid us; they are fragmentary and are either sterile or in poor condition." For this reason, Evans regards the species as inadequately founded, and drops it from consideration. Some years later, Evans (1911) described a species from the Bahamas, *Ceratolejeunea integrifolia*, and later during that year reported it from Florida, on the basis of specimens collected near Sanford, Fla., by Rapp.

Fulford (1945) reduced *Lejeunea laete-fusca* and *Ceratolejeunea integrifolia* to synonyms of *C. guianensis*. The latter species name is also taken up by Frye and Clark (1947) for the North American material. As regards the identity of *C. integrifolia* and *L. laete-fusca*, there is no doubt whatsoever about the correctness of this. The "species" have been compared carefully, and are identical in every respect. However, the writer totally fails to see the basis for the identification of our North American material with the South American *C. guianensis*. Furthermore, the South American material placed as *C. guianensis* by Fulford clearly includes two very distinct species. These three taxa are separable as follows:

1. Cells of the leaf-margins 15–17 μ, of leaf-apices and leaf-middle 18–20 or 20–24 μ up to 23–25 × 25–30 μ; branches with utriculi; South America and southern portion of West Indies ..... 2.
   2. Underleaves very large and distinctly imbricate, 380–520 μ wide (width 4–7 × the stem width; at least ⅓ × width of shoot), subcordate or cordate at base; autoecious. *C. confusa* sp. n. (Trinidad, W.I.).
   2. Underleaves small and distant, mostly 160–190 μ wide (width 1.8–2.5 × the stem width; no more than ⅙ × shoot width), rounded to base; ? dioecious. *C. guianensis* (type!)
1. Cells of the leaf-margins (9) 10–11 (12) μ, of the leaf-apices and leaf-middle 13–15 (16) μ; utriculi uniformly absent; underleaves small, less than 250–300 μ wide (width 1.5–2.9 × the stem width; no more than ¼ the shoot width), rounded or cuneate to base; dioecious ..... *C. laete-fusca*

It is, furthermore, the contention of the author that these three species are not even immediately related. Evans (1911) carefully noted the small size of the leaf-cells in his *C. integrifolia*, giving them as 9 μ on the margins, 15 μ in the middle, 15 × 18 μ at the base. These measurements are closely matched in the lectotype of *L. laete-fusca*: 9–11 μ on margins, 13.5–15 μ medially, 15 × 18–23 μ at base (just above the ocelli). By contrast, in both *C. confusa* and *C. guianensis* the marginal cells average 15–17 μ; the subapical, 18–20 μ; the median, 20–21 μ; the basal, 20–23 × 23–32 μ, or even slightly larger (in *C. confusa*). Fulford, in *C. guianensis*, gives the cells as 18 μ in the "apical region, . . . those of the rest of the leaf larger."[7] Since Frye and Clark give individual cell-meas-

[7] Stephani, in his unpublished *Icones*, also illustrates *C. guianensis*, from a specimen collected in "Guyana, Leprieur." He describes the cells as 18 μ wide apically, and 18 × 36 μ near the base; the ocelli are supposedly 36 × 54 μ. These plants, which are characterized as dioecious, bear perianths very similar to those of *C. laete-fusca* (and *C. confusa*), in that there are four weakly produced, angulate shoulders. Stephani illustrates the plants as having entire, acute or subacute lobes of the bracts; narrowly ovate to lanceolate lobules that are acute to subacute, otherwise edentate; a bracteole bilobed for only one-fifth its length.

urements, and do not distinguish between width and length, their measurements are meaningless.

Fulford (1945, p. 393) also states that utriculi are absent in *C. guianensis*. However the type material (*ex* herb. Montagne) she studied and annotated shows free development of the large utriculi! These do not occur at the bases of all branches, but where present are well-developed, and occur either singly or in pairs (Fig. XXIV: 1). In *C. laete-fusca* no trace of utriculi is apparently ever developed (Fig. XXIV: 11). Particularly in the latter species, the numerous available collections have been carefully examined for this feature, without success. Evans (1911, p. 214), in his careful analysis, also emphasizes the absence of utriculi as one of the distinctive features of his *C. integrifolia* (= *C. laete-fusca*). Until it can be shown that *C. laete-fusca* is able to develop utriculi, the writer prefers to follow Evans in assigning some systematic significance to their absence.

Ceratolejeunea guianensis and *C. laete-fusca* appear to agree in two important features, however. Both appear to be dioecious (certainly *C. laete-fusca* is constantly dioecious), and both have small, distant underleaves, little or no more than twice the width of the stem (Fig. XXIV: 1–2, 10–11). *Ceratolejeunea confusa*, of very different habit, is autoecious, and has extremely large, transversely suborbicular, imbricate underleaves (Fig. XXIV: 7–9). Although this species was referred to *C. guianensis*, it fails to key out as such in Fulford's key (1945), since it would key out to the first half of couplet *8* (p. 371).[8]

A further point of confusion introduced by Fulford (1945, p. 393) concerns the androecium. She describes this as "distinctive for the species in that the spike is broader and the bracts more spreading than in the other species." She claims that this is the case in both the "*guianensis*" and the "*integrifolia*" plants. However, a portion of the type (male only) of *C. guianensis*, *ex* herb. Hooker (NYBG), shows a lateral spicate androecium, with 7–8 pairs of bracts (not the 3–6 pairs she describes). Furthermore, the bracts are erect, closely imbricate, strongly saccate, with the spike only 400–420 μ broad. There is not the slightest difference in appearance between such an androecium and that of *C. cubensis*, for example.

Perhaps most confusing in her discussion is the statement: "Whenever perianths have been found they, too, have been identical—without horns—on both types of plants" (e.g., the pigmented "*guianensis*" type, and the less deeply pigmented "*integrifolia*" type). However, the type specimen of *C. guianensis* available (studied by Fulford and myself) does not show perianths.[9] The type plants of *C. integrifolia* do not show perianths, and the lectotype of *C. laete-fusca* is sterile.[10] Consequently, the meaning of this statement is unclear to the

[8] It is to be noted that this specimen served for the sporeling studied in Fulford, 1944. Consequently the data there given are to be attributed to *C. confusa*, rather than to *C. guianensis*.

[9] Admixed, however, is a perianth-bearing plant referable to *Cheilolejeunea rigidula*.

[10] Typical material of *C. laete-fusca*, from Florida, shows shorthorned perianth keels, and is deviant in having a fifth, although weak, dorsal keel. This material, although studied (and annotated) by Fulford, does not fully agree with the figures or descriptions in Fulford (1945, p. 392–393).

writer. The type of the very different *C. confusa* (= *C. guianensis* Fulford, in part, nec Montagne) is provided with perianths, and these agree with those figured for the "*C. integrifolia*" type by Fulford. What the perianths of typical *C. guianensis* are like is at present not clear.

From the preceding it is clear that *C. guianensis* Fulford is a composite species. Of the three species involved, *C. laete-fusca* differs from *C. guianensis* in (1) absence of utriculi; (2) much smaller leaf-cells; (3) less compact androecia; (4) generally more olive-brown pigmentation. The species name, *laete-fusca*, referring to the warm or "cheerful" brown color is quite appropriate, since it is in contrast to the much deeper brown of the type plants of *C. guianensis* (and the scorched brown of *C. confusa*).

DIFFERENTIATION.—*C. laete-fusca* is an excellently characterized species, closely allied to *C. cubensis*. It agrees with this species in the orientation of the ocelli in a basal group of usually 2–3, rarely 4 or 5–7, in the form of the underleaves, in the general facies and color, and in robustness. However, *C. laete-fusca* has constantly entire leaves, usually evenly rounded (rarely, isolated leaves obtusely pointed); it is dioecious; it has considerably smaller leaf-cells; it never possesses utriculi; and it has a perianth with the keels only obscurely developed as horns.

The perianths of this species have never previously been described.[11] They differ from those of our other two species in that there are five distinct carinae, the dorsal often weaker than the others and short. The lateral and ventral carinae are produced as rather weak crests. These crests are sharply compressed, wing-like, and vary from rectangulate to somewhat acute; the very apices may be very narrowly rounded off. In most cases the crests are produced merely to about the level of the apex of the recessed beak; in other cases they extend upward for a short distance beyond the beak. In no case have crests been observed as high as those in *C. cubensis*, nor are they normally as sharp. In both species the "horns" are not inflated or scarcely so, but are rather compressed, and wing-like in appearance. The fifth keel may be obtusely angulate in a few cases; usually it gradually disappears towards the beak. The presence of such a fifth, antical keel is noteworthy in a genus that is always characterized as having 4-keeled perianths. It places the species very low in the genus.

The ocelli of *C. laete-fusca* are usually two (then almost always lying side by side) or three (in which case the third ocellus often lies anterior to, and separated by a vegetative cell from, the paired ocelli). However, other modes of arrangement are not uncommon. Not infrequently, well-developed plants show a fourth ocellus, but it is exceptional to find a larger number of ocelli. Such an exception is formed by the extremely robust plants (up to 1100 μ wide) from Hillsborough River, Fla. (*Schuster 33940*). In these there may be only 2–3 ocelli, at the bases of some leaves, while others have a group of four or five. In a few

[11] The figures (Figs. 86, 87) in Fulford (1945) may or may not belong to this species. At any rate, they do not show the development of obtusely angular horns, which is characteristic of this species. The present description is based on plants from Shields Hammock, Dade Co., Fla. (*Small, Mosier and Small 6158*).

cases there are even 6–7 ocelli, arranged in a proximal and a distal tier; in such cases, of course, the ocelli are not equidistant from the leaf-base. Such exceptional cases should not cause confusion with the pluriocellate *C. rubiginosa*. However, a few young leaves among the plants of this collection showed two ocelli at the base, forming a short line. Such instances mark a transition to weak forms of *C. rubiginosa*, in which there may be only 2–3 ocelli forming a short vitta. The ocelli in the preceding plants also deviate from the "norm" in *C. laete-fusca* in often attaining a much larger size. Frye and Clark (1947) attempt a separation between *C. laete-fusca* (their *C. guianensis*) and *C. cubensis* on that basis, citing the ocelli of the former as "about 16 by 35 μ," of the latter as "about 27 by 45 μ." Schuster and Hattori (1954) narrow these differences down, *C. laete-fusca* being cited as with ocelli "usually 18–20 × 36–40 μ," whereas in *C. cubensis* they are given as "20–21 × 38–40 μ, occasionally 22 × 45 μ." However, the ocelli in robust plants of *C. laete-fusca* may be 25 × 45 μ, or in exceptional cases even 26 × 55 μ. There is, therefore, no valid constant basis here for attempting a separation of two species.

Ceratolejeunea confusa sp. n.[12]

Ceratolejeunea guianensis Fulford, Bull. Torrey Bot. Club. **71**: 646, figs. 44–54 (spores and sporelings), 1944 (not of Stephani, 1913); Fulford, Brittonnia **5**: 391, 1945 (in part; not of Stephani, 1913).

Monoica; mediocris; fusco-brunnea; major. Caulis ad 1250 μ latis. Folia caulina imbricata, concava, ovata-oblonga (ca. 600 μ longa × 500 μ lata), apice rotundata, integra, decurva. Lobulus exiguus, folio quadruplo brevior, ovatus; utriculus majusculus. Cellulae superae et marginalis 17–18 μ, trigonis magnis. Amphigastria caulina magna, caule quadruplo-quintuplo latiore, subrotunda, ad ⅓ inciso-biloba, lobis triangulatis acutis. Folia floralia obovato-oblonga, apice late rotundata. Perianthia obovata-obpyriformia, apice breviter quadri-umbonata, umbonis late triangulatis obtusis, rostro valido.

Plants shiny, in depressed patches, *intensely brownish tinged*. Shoots 1000–1250 μ wide, rather freely but irregularly pinnate, the branches wide-spreading, never microphyllous; stems 80–100 μ in diameter, the ventral cortical cells *ca.* 35 μ wide. Leaves *closely imbricate, distinctly concave*, asymmetrically oblong-ovate, widely spreading, *distinctly falcate*, both antical and postical free margins arched into the *broadly rounded*, entire-margined apex, up to 500 μ wide × 600 μ long (from base of keel). Lobule small (*ca.* 100–110 μ wide × 130–150 μ long) but strongly inflated, the basal portion almost spherical, constricted near apex, the slightly flaring apex appearing nearly truncated, bearing a *short and acute or subacute apical tooth* (which is only 17–20 μ long, hardly longer than broad). One, or sometimes two basal leaves of some, but not all, branches modified to form *prominent utriculi*. *Underleaves closely imbricate, very large* (averaging 4–5 (6–7) times as broad as stem on mature shoots), up to 440–450 μ wide × 380–400 μ long, occasionally 500–520 μ wide × 375–400 μ long, subcordate to rounded-cordate at the base, *averaging 1.1–1.3 × as wide as long*, their lobes usually (10) 12–15 cells broad at base, acute or subacute, the open sinus acute; *rhizoids* very few, the *rhizoid-initial disks very small, obscure*. Cells *relatively large*: marginal

[12] The species name is deemed peculiarly appropriate since the plants ascribed to this taxon have been confused with *C. guianensis*.

(15) 17–18 μ; median varying from (21) 23–25 × 25–30 μ; basal cells, peripheral to ocelli, 20–25 × 28–36 μ; mature plants with large trigones and strong elliptical intermediate thickenings (which are almost coalescent, leaving only small pits), the walls pigmented deep brown. *Ocelli 1–2 per leaf-base*, situated side-by-side, the larger ocellus 25–30 × (40) 55–60 μ, relatively thin-walled.

Autoecious. Androecia usually on leading, leafy shoots, sometimes on more or less leafy, but short, lateral shoots, 500–600 μ wide, compactly apicate, of usually 3–6 pairs of bracts, terminal, with a single bifid bracteole at base. Gynoecia usually on short lateral branches, each with a single innovation. Bracts large, the mature perianth only 0.2–0.3 emergent; lobe of bracts obovate, *usually* broadly rounded at apex, rarely subacute, *entire-margined*, *ca.* 420–450 μ wide × 650–670 μ long; lobule variable, from obovate and broadly truncate-repand-dentate at apex to ovate-lanceolate and sharply acute-subacuminate at apex, 250–275 μ wide × 500–580 μ long; keel short (220–300 μ), sometimes irregularly winged. Perianth obpyriform to obovoid, *ca.* 430–460 μ wide above the middle × 670–850 μ long, rather sharply 5-carinate in the distal one-third or one-fourth (the antical keel less distinct), the carinae crenulate from bulging cells, *rounded into the rounded-truncate perianth-apex without trace of development into horns* (the lateral and postical carinae at most slightly compressed and dilated), bearing a rather elongate beak formed of 3 tiers of cells (the terminal tier of strongly elongate cells, *ca.* 9 × 25–30 μ).

TYPE.—Caroni north bank road, Trinidad (*E. G. Britton, D. Coker, W. R. Rowland*, March 21, 1920); in herbarium of NYBG, with slides in writer's herbarium. Known only from the type collection.

DIFFERENTIATION.—Fulford (1944, 1945) confused this strongly isolated species with *C. guianensis*, and *C. laete-fusca*. However, it bears no immediate affinity to either of these species. It differs from both of these species in several obvious respects, among them (1) the very large, transverse, imbricate underleaves, whose lobes are normally 10–12 cells wide at base, or more; (2) the five-carinate, but wholly unhorned perianth, which is rounded to truncate at the apex, with the beak elongate and not recessed; (3) the more strongly concave leaves, quite obviously falcate in form; (4) the broadly rounded and wholly entire-margined lobes of the female bracts. The distinctive underleaves are alone sufficient to remove the species from the affinity of these two species.

Ceratolejeunea confusa shows additional differences from these two species that deserve emphasis: it differs from *C. laete-fusca* in addition in (1) the larger leaf-cells, with trigones and intermediate thickenings more obviously developed; (2) the presence of well-developed utriculi at the bases of some branches; (3) the deeper brown color and larger size; (4) the more imbricate leaves and underleaves; (5) autoecious inflorescence.

Ceratolejeunea confusa differs, in addition, from typical *C. guianensis* in the following points: (1) autoecious inflorescence; (2) androecia normally on elongated, normal leafy shoots, rarely on short lateral branches.

Although the material of this species was referred to *C. guianensis* in Fulford (1945) it keys in that work clearly to *C. grandibracteolata*, with which it agrees in such key characters as: "Leaves rounded, entire; underleaves orbicular . . . large, several times broader than stem; . . . plants robust, deeply pigmented; apical tooth of lobule short, straight to slightly curved; . . . leaves persistent

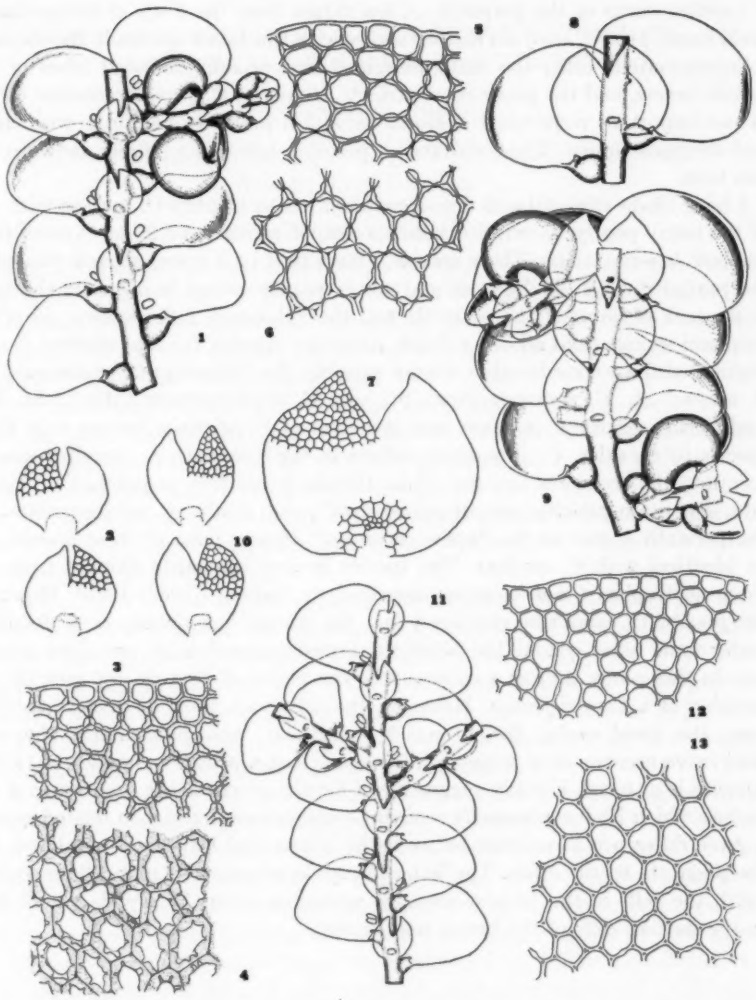

FIG. XXIV. *Ceratolejeunea guianensis* (Mont.) Schiffn. 1. Postical aspect of shoot-sector, with utriculi-bearing branch (× 33); 2. Underleaves (× 75); 3. Marginal cells of leaf apex (× 275); 4. Median cells of lobe (× 275). *Ceratolejeunea confusa* Schust. 5. Marginal cells of lobe apex (× 275); 6. Median cells of lobe (× 275); 7. Normal-sized underleaf (× 75); 8. Shoot-sector, postical view (× 33); 9. Shoot-sector, postical view, with two utriculi-bearing branches (× 33). *Ceratolejeunea laete-fusca* (Aust.) Schust. 10. Underleaves (× 75); 11. Shoot, postical view (× 33); 12. Marginal cells, leaf-apex (× 275); 13. Median cells of lobe (× 275). (Figs. 1–4, drawn from type of *C. guianensis* (NYBG); 5–9, drawn from type of *C. confusa* (NYBG); 10–13, *C. laete-fusca*, from Costello Hammock, Dade Co., Florida, *Schuster 22964*).

. . . entire; horns of the perianth . . . low ridges from the keels of the perianth; ocelli basal, 1–3." *C. confusa* further agrees with this latter species in the strongly collenchymatous cells; the entire-margined and broadly rounded lobes of the female bracts, and the presence of utriculi. However, *C. grandibracteolata* differs in two important respects: it is dioecious, and it possesses perianths with sharp and divergent horns. These differences prohibit any closer affinity between the two taxa.

I have made repeated and unsuccessful efforts to identify *C. confusa* with one of the many poorly known Stephani species, of which some 28 are known from tropical America alone. These species, except in 4 or 5 cases, are not treated in the partial revision by Fulford, and are extremely poorly known. On the basis of the lack of horns of the perianth, and the autoecious inflorescence, all of the Stephani species (and all other South American species, for that matter) can be eliminated from consideration, except possibly the following: *C. granatensis* St., *C. mosenii* St., *C. scaberula* (Spr.) St., and *C. splitbergeriana* (Mont.) St. Fulford (1945) regards *C. mosenii* as a synonym of *C. cubensis*, leaving only three species to consider. *C. granatensis* differs in the "perianth . . . breviter quadricornute;" *C. scaberula* has the "folia floralia perianthio aequilonga . . . apiculata, superne regulariter remoteque dentata"; and, finally, *C. splitbergeriana* has the perianth angles at the "apice cornutus." Hence, none of these species can be identical with *C. confusa*. The species is very obviously distinct from the three neotropical *Ceratolejeuneae* described by Herzog ([1942] 1945). However, the possibility cannot be dismissed that the species has already been described under some other genus! The wholly unarmed perianth-keels are quite anomalous in this genus, and as a consequence the plants at first do not give the impression of a *Ceratolejeunea*. However, the cells with their distinctive thickenings, the basal ocelli, the brownish coloration, and particularly the very distinctive occurrence of utriculi, all suggest that a primitive species of *Ceratolejuenea* is at hand. Equally suggestive of *Ceratolejeunea* is the occurrence of one feature which I have repeatedly seen in *Ceratolejeunea*, but not in related genera: a gross difference in cell-size between the bracts and leaves, on one hand, and the perianth, on the other. The latter always is prominently more "large-celled" (with the cells in the present instance averaging about 35 μ wide vs. 23–25 μ in the median cells of the bracts and leaves).

TAXONOMIC REVISION OF THE GENUS *NUPHAR* SM. OF NORTH AMERICA AND EUROPE[1]

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Introduction

The genus *Nuphar*, as restricted by Smith (1809), includes only the Yellow Water-Lilies of the "luteum" group; the White Water-Lilies being retained in the Linnaean genus *Nymphaea* (as emended by Smith). Despite numerous, and often heated, arguments concerning the legality of recognizing Smith's taxon, the genus *Nuphar* Sm. is now established as a *nominum conservandum* in the International Code of Botanical Nomenclature (Lanjouw, 1952, p. 102).

Morong (1886) revised the North American representatives of *Nuphar*, recognizing five species. Schuster (1906, 1907–08) discussed the numerous European variations of *Nuphar* and, although acknowledging the existence of intermediate forms, recognized two species. Miller and Standley (1912) presented a detailed taxonomic study of the North American Yellow Water-Lilies, recognizing seventeen species and two subspecies.

The abundance of forms intermediate between recognized taxa and the consequent disagreement concerning the taxonomic treatment of natural populations of *Nuphar* have led to this present attempt to understand the genus.

During the summer of 1952, field observations and collections were made in southern Georgia, northern Florida and South Carolina. Collections of *Nuphar* in the Missouri Ozarks, southern Illinois and Iowa were made during the summers of 1952–53, and in North Carolina during the summer of 1955.

In order to determine the geographical distribution and morphological variation within the genus, slightly more than four thousand specimens of *Nuphar* were examined. Included in these specimens were seven holotypes, four syntypes, one paratype and one topotype of the nineteen taxa recognized by Miller and Standley (1912). The preserved type material of one species and one subspecies was not obtained and type material of the four remaining species is not known to exist. Of the four taxa described since the treatment by Miller and Standley, two holotypes, one isotype and one topotype have been examined. Although there has been no designation of type material in the majority of specific and infraspecific epithets assigned to the Yellow Water-Lilies, especially in the European taxa, a large number of epithets have been authenticated through exsiccati or as collections by the author who first published the name concerned. The original publication of each specific or infraspecific epithet, included either as a recognized taxon or as a synonym, has been consulted, except where indicated otherwise.

[1] Based upon a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Botany of the State University of Iowa, 1955.

In coal of the Jurassic age at Brora, Sutherlandshire [sic], Scotland, Simpson (1937) has identified pollen grains of the *Nelumbo* Adans. (as *Nelumbium*) and *Nymphaea* L. (as *Castalia*) types. Although pollen of *Nuphar* was not identified in this coal deposit, one can assume that these plants are also of ancient origin.

The isolated nature of aquatic habitats, in conjunction with an infinite capacity for vegetative reproduction and the ancient status of the Nymphaeaceae, has resulted in the establishment of innumerable populations of *Nuphar* which exhibit various combinations of distinctive features. Although the features of the various taxa were found to be relatively consistent within their respective geographical and ecological limits, morphological variability within the total range of the genus is enormous and non-disjunctive. In some areas of geographical overlap of ranges there is a gradual transition from one taxon to another; in others an erratic exchange of features. Sterility of transitional forms, although reported in some populations, is by no means universal. Without doubt, many populations of *Nuphar* are genetically incapable of interbreeding, but the existence of numerous transitional forms in areas of range overlap and the sporadic occurrence of some of the more characteristic features of one taxon within the range of another raises the question of such a barrier as evidence of specific rank for the taxa concerned.

The taxa under consideration thus fall most nearly into Clausen's (1951) characterization of "ecospecies," each consisting of numerous local variants. Since the formal recognition of all variants and transitional forms of *Nuphar* is not feasible, the identity of only those morphological variants that coincide with geographical and ecological features are here considered as subspecies. This seems to be in accord with Babcock's (1947) concept of a polymorphic species which he describes as follows: "[A polymorphic species may consist of many] . . . subspecific groups, occupying different but usually overlapping geographic areas. These subspecies differ more from one another in structure and interfertility or both than do the individuals composing each subspecies, but the subspecies are sometimes still connected with one another by intergrading forms. This is the necessary result of genetic variability within the species, plus the influence of environmental variability, isolation and natural selection or random fixation. It is a stage in one process of species formation."

The genus *Nuphar*, as it occurs in North America and Europe, is here considered to consist of one polymorphic species, *N. luteum*, with nine recognizable subspecies distributed as follows: In lower altitudes and latitudes of Eurasia, subsp. *luteum*; in higher altitudes and latitudes of Eurasia and in northeastern North America, subsp. *pumilum*;[2] in ponds of northern United States and Canada, subsp. *variegatum*; in flowing water or tidal mud-flats of freshwater streams (occasionally in ponds) throughout eastern United States and extending southward into Mexico and Cuba, subsp. *macrophyllum*;[3] in the tidal reaches of

[2] The North American representatives of this subspecies are more familiarly known as *N. microphyllum*.

[3] These highly variable plants have been previously treated as *N. advena*.

streams in Virginia and the Carolinas, subsp. *sagittifolium*; in acidic ponds of the Coastal Plain in Georgia and northern Florida, subsp. *orbiculatum*; in the Blackwater River of western Florida, subsp. *ulvaceum*; in the Ozark region of Missouri and adjacent Arkansas, subsp. *ozarkanum*; and in northwestern North America, subsp. *polysepalum*.

Scarcity of material from southeastern China and Japan has prevented a determination of the position of those plants within the genus *Nuphar*.

Neither chromosome number (in all forms that have been examined, the haploid number is 17) nor pollen morphology appears to be of any aid in distinguishing the taxa of *Nuphar*. A comparative study of seedling development in four subspecies of *N. luteum*, however, has shown some correlation between recognizable taxa and developmental patterns. More intensive study along these lines is now being undertaken in the hope that differences in seedling characteristics may prove to be of importance in distinguishing the taxa.

The extent to which expressed characteristics result from apomixis, ecological selection, random fixation or direct environmental control has not been determined.

Herbarium specimens of *Nuphar* are notoriously incomplete and measurements of dried specimens are considered too inaccurate to allow a critical analysis of variation. Therefore, no detailed comparisons are presented in this paper. However, intensive field studies of selected populations of *Nuphar* are in progress.

ACKNOWLEDGEMENTS

The writer wishes to thank the curators of the following herbaria for their generous loan of specimens. The symbols are those of Lanjouw (1954) and will be used in the citation of representative specimens. Of the total number of specimens examined, only a few are cited in this paper. A complete list, except those of MSC, MT and SMU, may be found in the original dissertation (Beal, 1955). Cornell Univ. (CU); Duke Univ. (DUKE); Chicago Museum of Natural History (F); Florida Agri. Exp. Sta., Gainesville (FLAS); Conservatoire et Jardin Botaniques. Geneve (G); Univ. of Georgia (GA); Gray Herbarium (GH); Univ. of Iowa (IA); Univ. of Illinois (ILL); Royal Botanic Gardens, Kew (K); Univ. of Michigan (MICH); Univ. of Minnesota (MIN); Missouri Botanical Garden (MO); Michigan State College (MSC); Herbier Marie-Victorin (MT); North Carolina State College (NCSC); Univ. of North Carolina (NCU); Tulane Univ. (NO); New York Botanical Garden (NY); Muséum National, Paris (P); Univ. of Wyoming (RM); Naturhistoriska Riksmuseum, Stockholm (S); Southern Methodist Univ. (SMU); Univ. of Texas (TEX); Univ. of Arkansas (UARK); Univ. of California (UC); National Museum, Washington (US); Univ. of Wisconsin (WIS).

An expression of gratitude is offered to Prof. R. F. Thorne, not only for making available the facilities of the Herbarium of the State University of Iowa, but also for technical aid and patient encouragement.

For the opportunity to collect in Georgia and Florida, I am deeply indebted

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SYSTEMATIC TREATMENT

Nuphar Sm.

Sibth. & Sm., Fl. Graec. Prodr. **1:** 361. 1808 (1809).

Nymphaea L. Sp. Pl. p. 510. 1753. (In part.)
Nymphaea Salisb. *in* Konig & Sims Ann. Bot. **2:** 71. 1806.
Nymphozanthus Rich. Demonstr. Bot. May, 1808. (On pages 63 and 103 spelled "Nymphozanthus", on page 68 as "Nymphosanthus".)
Nenuphar Hayne, Gertreue Darstel. und Beschgreig. Arzneyk. 4. t. **36:** 1816.
"*Nymphanthus* Rich." Desv. Obs. Pl. d'Angers, p. 84. 1818.
"*Nymphosanthus* Rich." Desv. Fl. l'Anjou, p. 80. 1827.
Clairvillea Hegetschweil. *in* Labram & Hegetschweil. Samml. Schweiz. Pflanz. t. **21:** 1826–34.
Blepharia Sm. Mem. & Corr. **1:** 576, 1832.
Ropalon Raf. New Fl. N. Amer. **2:** 17. 1836. (Part 2 is reported to have been published in the second half of 1837 by J. H. Barnhart in Torreya **7:** 177–181. 1907.)
Nenufar Peterm. Fl. Lips. exc. p. 395. 1838.
Nufar Wallr. Erst. Beirt. Fl. Hercyn. p. 212. 1840.
"*Nyphar* Sm." Wapl. Rep. Bot. Syst. **1:** 108. 1842.
Nymphona Bubani, Fl. Pyren. **3:** 259. 1901.

DESCRIPTION.—Perennial aquatics with procumbent, branching rhizomes, the older portions of which decay, thus isolating progressively more numerous growing tips. Leaves spirally arranged, with cylindric, flattened or winged petioles attached to the blades at the base of a deep sinus. Blades entire, pinnately veined, lanceolate to orbicular, glabrous above and glabrous to densely pubescent below: emersed, floating or submersed, the latter thin and delicate. Petioles and peduncles glabrous to pubescent, containing an abundance of astrosclereids with two to five forks extending into each adjacent intercellular air space. Sepals 5–14, greenish, yellow- or red-tinged, persistent. Petals numerous, thick and oblong to thin and spatulate, often emarginate. Stamens numerous, yellow- or red-tinged, attached in spiral rows below the gynoecium; maturing centripetally, recurving and exposing the anthers. Pollen grains monocolpate, oblate-spheroidal, 40–71μ in length and 30.4–60μ in diam.; the exine with abundant spinoidal projections 3.2–9.6μ in length. Gynoecium of fused carpels, the stigmatic rays few to many, permanent, borne on an entire to dentate, greenish, yellow- or red-tinged disk which is more or less separated from the greenish, yellow- or red-tinged body by a constriction; usually ripening above water. Seeds numerous, narrowly to broadly ovoid, yellow to brown, with a more or less conspicuous raphe and opening by a small operculum. Embryo with two fleshy cotyledons, closely invested by a thin covering of endosperm and embedded in abundant perisperm.

TYPE SPECIES: *Nuphar luteum* (L.) Sibth. & Sm.

Generic distinction between the Yellow and the White Water-Lilies, both of which were included in the Linnaean genus *Nymphaea*, was first recognized by Salisbury in 1806, the Yellow Water-Lilies being retained in the genus *Nymphaea*. The name *Nuphar*, applied by Smith to this taxon in 1809, is, however, retained as a *nominum conservandum*.

An examination of herbarium and living specimens has demonstrated such a close morphological relationship among the previously recognized North American and Eurasian species that it is advisable to recognize only those forms that are associated with geographical or ecological features. The nine taxa concerned are thus reduced to subspecific rank within *N. luteum*.

Nuphar luteum (L.) Sibth. & Sm.

Fl. Graec. Prodr. **1:** 361. 1808 (1809).

DESCRIPTION: Plants extremely variable. Floating or emersed leaves glabrous to densely pubescent below; rounded to acute at the apex; lobes overlapping to widely divergent, with broadly rounded to acute tips; petiole glabrous to densely pubescent, terete to strongly winged. Sepals 5–14. Anthers 1–8 mm. long. Fruit narrowly to not at all constricted below the dentate to entire stigmatic disk. Seeds up to 6 mm. long.

It may be noted that the descriptions of the following subspecies overlap in many instances and many intermediate specimens, exhibiting any combination of features, are to be expected. Consequently, any decision to assign an intermediate plant to either of the involved subspecies must be arbitrary. Plants intermediate between *N. luteum* subsp. *luteum* and *N. luteum* subsp. *pumilum*, as well as between the latter and *N. luteum* subsp. *variegatum*, are especially abundant in areas where ranges of the taxa concerned overlap and have received much attention in the past. Therefore, they are recognized, not as subspecies, since their habitat is essentially the same as that of their supposed parents, but as putative hybrids.

Nuphar luteum subsp. *macrophyllum* is interpreted in an especially broad sense, including those plants which exhibit characteristics passing into closely associated subspecies.

No attempt to describe all the minor variations observed within a taxon has been made.

KEY TO THE SUBSPECIES

1. Fruit narrowly constricted below the stigmatic disk; petals mostly thin and broadly spatulate; sepals usually 5.
   2. Stigmatic disk entire or slightly crenate; anthers mostly 3–7 mm. in length
      1. subsp. *luteum*
   2. Stigmatic disk deeply crenate or dentate; anthers mostly 1–2 mm. in length
      2. subsp. *pumilum*
1. Fruit only slightly or not at all constricted below the stigmatic disk; petals mostly thick and oblong; sepals usually 6–12.
   3. Exposed leaf blades more than twice as long as wide, the sinus less than ¼ the length of the blade.

4. Blades lanceolate to linear, 3–5 times as long as wide, the lobes usually not overlapping; sepals mostly 6; stigmatic rays linear
5. subsp. *sagittifolium*

4. Blades lanceolate, about 2½ times as long as wide, the lobes commonly overlapping; sepals 6–9; stigmatic rays more or less elliptical
6. subsp. *ulvaceum*

3. Exposed leaf blades less than twice as long as wide, the sinus relatively deeper.
5. Petiole conspicuously flattened and winged on the upper surface; sepals usually red-tinged within..... 3. subsp. *variegatum*
5. Petiole terete to more or less flattened on the upper surface; sepals green, yellow or red-tinged within
6. Sepals commonly 9 (7–12); seeds usually narrowly ovoid. Anthers commonly red-tinged, sometimes yellow..... 9. subsp. *polysepalum*
6. Sepals normally 6; seeds usually broadly ovoid.
7. Inner portions of the sepals conspicuously red-tinged; fruit variously red-tinged. Leaves mostly floating..... 7. subsp. *ozarkanum*
7. Inner portion of the sepals green to yellow (rarely red-tinged). Fruit green (rarely red-tinged). Leaves floating or erect.
8. Leaf blades densely pubescent below, thick and leathery, orbicular or nearly so, with broadly rounded lobes; floating
8. subsp. *orbiculatum*
8. Leaf blades glabrous to more or less pubescent, ovoid or nearly so, the lobes widely diverging and acute to overlapping and broadly rounded; erect or floating..... 4. subsp. *macrophyllum*

1. *N. luteum* subsp. *luteum*

Nymphaea lutea L. Sp. Pl. p. 510. 1753. (In part.)
Nymphaea umbilicalis Salisb. *in* Konig & Sims Ann. Bot. **2:** 71. 1806.
Nuphar lutea Sibth. & Sm. Fl. Graec. Prodr. **1:** 361. 1808 (1809).
Nymphozanthus vulgaris Rich. Ann. Mus. Hist. Nat. **17:** 230. 1811.
Nenuphar lutea Hayne, Getreue Darstel. und Beschreib. Arzneyk. IV, t. **36,** 1816.
Nymphanthus europaeus Desv. Obs. Pl. d'Angers, p. 84. 1818.
Nuphar lutea DC. Reg. Veg. Sys. Nat. **2:** 60–61. 1821. (In part).
Nuphar sericeum Láng, Syl. Ratisb. **1:** 180. 1824.
Nuphar spathulifera Rchb. Icon. Bot. seu Pl. Cr. **2,** p. 10. 1824.
Nuphar tenella Rchb. *ibid.*
Nymphosanthus europaeus Desv. Fl. l'Anjou, p. 80. 1827.
Nuphar minor Dum. Fl. Belg. Prodr. p. 131. 1827.
Nuphar lutea β sericea Spenner, Fl. Friburg. **3:** 985. 1829.
Clairvillea lutea (L.) Hegetschweil. *in* Labram & Hegetschweil. Samml. Schweiz. Pflanz. t. **21,** 1826–34. (*Non-viso*; *fide* Fernald, Rhodora **21:** 186. 1919).
"*Nenufar luteum* Hayn." Peterm. Fl. Lips. exc. p. 395. 1838.
"*Nenufar tenellum* Rchb." Peterm. Fl. Lips. exc. p. 396. 1838.
Nufar systylum Wallr. Erst. Beitr. Fl. Hercyn. p. 212. 1840. (*Non-viso*; *fide* Fernald, Rhodora **21:** 186. 1919).
Nuphar luteum var. *urceolata* Casp. *in* Walpers Ann. Bot. Syst. **4:** 168. 1857.
Nuphar luteum var. *rubropetalum* Casp. Schrift. Konig. Phys.-Okon. Gesells. Konigs. **2:** 49–50. 1861 (1862).
Nuphar confusum Gandoger, Fl. Gallic exs. no. 187. 1879.
Nuphar luteum β minus Čelakovský, Prodr. Fl. Böhmen, **4:** 854. 1881.
Nymphaea lutea f. *terrestris* Clavaud, Fl. Gironde, p. 264. 1881. (*Non-viso*; *fide* Schuster, 1908, p. 68).
Nuphar luteum β genuinum Coutinho, Boletim da Sociedade Broteriana, **10:** 90. 1892 (1893).
Nuphar luteum β punctatum Coutinho, *ibid.*
Nuphar luteum β submersum Rouy & Foucaud, Fl. Fr. **1:** 149. 1893.

Nuphar sericeum var. *denticulatum* Harz, Botan. Centralbl. **53:** 226. 1893.
Nuphar luteum var. *purpureosignatum* Hisinger, Acta Soc. Fauna Flora Fenn. **11**(9). 1895.
Nymphona lutea (L.) Bubani, Fl. Pyren. **3:** 260. 1901.
Nuphar schlierense Harz, Fl. exs. Bavarica no. 404. 1901.
Nymphaea lutea var. *genuina* (Coutinho) Schuster, Bull. Herb. Boiss. ser. 2. **8:** 68. 1908.
Nymphaea lutea var. *genuina* f. *punctata* (Coutinho) Schuster, *ibid.*
Nymphaea lutea var. *genuina* f. *purpureosignata* (Hisinger) Schuster, *ibid.*
Nymphaea lutea var. *genuina* f. *tenella* (Rchb.) Schuster, *ibid.*
Nymphaea lutea var. *genuina* f. *urceolata* (Casp.) Schuster, *ibid.*
Nymphaea lutea var. *harzii* Schuster, Bull. Herb. Boiss. ser. 2. **8:** 69. 1908.
Nymphaea lutea var. *puberula* Schuster, *ibid.*
Nymphaea lutea var. *puberula* f. *schlierensis* (Harz) Schuster, *ibid.*
Nymphaea lutea var. *puberula* f. *sericea* (Láng) Schuster, *ibid.*
Nymphaea lutea var. *puberula* f. *sericea* sf. *denticulata* (Harz) Schuster, *ibid.*
Nuphar luteum var. *genuinum* f. *purpureosignatum* (Hisinger) Hegi, Ills. Fl. Mitt.-Europ. **3:** 445. 1912.
Nuphar luteum var. *genuinum* f. *submersum* (Rouy) Hegi, *ibid.*
Nuphar luteum var. *genuinum* f. *urceolatum* (Casp.) Hegi, *ibid.*
Nuphar luteum var. *puberulum* f. *sericeum* sf. *denticulatum* (Harz) Hegi, Ills. Fl. Mitt.-Europ. **3:** 446. 1912.
Nuphar luteum var. *affine* f. *parviflorum* Hegi, *ibid.* (*Nomen nudum*).
Nymphozanthus luteus (L.) Fern. Rhodora, **21:** 185. 1919.
Nymphozanthus sericeus (Láng) Fern. Rhodora, **21:** 187. 1919.
Nuphar luteum f. *submersum* Glück *in* Pascher, Die Suswasser-Flora Mitteleuropas, **15:** 252. 1936. (Without Latin diagnosis).
Nuphar luteum f. *terrestre* Glück, *ibid.* (Without Latin diagnosis).

TYPE SPECIMEN: In the Herbarium of Linnaeus (LINN). (See S. Savage, Catalogue of the Linnaean Herbarium, No. 673, p. 92. 1945.)

DESCRIPTION.—Exposed leaves floating, ovate, with approximate to overlapping lobes; glabrous to more or less pubescent below. Petiole more or less flattened and acutely angled above. Flowers 3–6.5 cm. in diam. Sepals mostly 5. Petals thin and broadly spatulate, mostly longer than the stamens. Anthers 3–7 mm. long. Fruit with a narrowly constricted neck below the entire to more or less crenate disk. Stigmatic rays 5–28, mostly ending 0.5–1 mm. from the disk margin. Seeds numerous, ovoid, about 5 mm. long and 3.7 mm. wide.

DISTRIBUTION.—(Map 4) Throughout almost all Europe except in the far north; south to La Calle (Algeria), Palestine and Iran; eastward in central Asia to southern Siberia and Manchuria (a specimen of this subspecies in the Muséum National d'Histoire Naturelle, Paris, labelled "Chaffanjon, 1896, Mandchourie" is presumably from Manchuria and represents the easternmost known station).

The large size of the flowers and leaves, as well as the large petals, elongate anthers and more or less entire stigmatic disks make this subspecies easily recognized throughout most of its geographical range. These characteristics are variable in Scotland, Switzerland and adjacent areas of France and Germany, western Czechoslovakia, Scandinavia and the Baltic areas of Europe and pass into *N. luteum* subsp. *pumilum*.

Of 266 specimens examined, the following have been selected as exhibiting a wide geographical and morphological range: **Algeria:** La Calle, 1918, *A. Clave* (G). **Belgium:** Limbourg, 1864, *Herb. A. Wesmael* (G). **Czechoslovakia:** Sobeslav, 1917, *H. Glück* (US).

Denmark: Ljole i Mosen V. for Jonstrup, 1894, *H. Mortensen* (US). **England.** CHESHIRE CO.: Oakmere, 1886, *A. Lomax* (MIN, NY, US). **Finland:** Kyrkslätt, in lacu Storträsk prope praedium Getberg, 1910, *E. Lindström 647* (G, MO, NY, P, UC). **France:** Charette, 200 m. elev., 1923, *L. de Chamberet 4365* (G, MT). **Germany:** RHEINPROVINZ, Graeben bei Kempen, 1874, *A. Vigener* (G, MICH, NY). **Hungaria:** In aquis stagnantibus profundis prope Huszt, *Vágner 2055* (G, MO, NY, US). **Iran:** Kermanshah, 1867, *C. Haussknecht 34* (G). **Ireland:** Ditches near Belfast, 1874, *S. A. Stewart 4173* (NY). **Lebanon:** Ras el-Ain, 1867, *C. Haussknecht* (G). **Netherlands:** De Eem, 1910, *M. Schoute* (US). **Palestine:** Jaffa, 1–20 m. elev., 1908, *Meyers & Dinsmore 4244* (G). **Poland:** 1938, *J. Karpinski 320* (GH, MO, MT, S, US). **Portugal:** Arredores de Coimbra, 1891, *A. Moller 1200* (G). **Scotland:** FIFE CO.: Dunfermline, 1853 (MICH). **Sweden:** KOPPARBERGS LÄN: Hedemora, in lacu Munkbasjön, 1933, *G. Ringselle 803* (G, GH, MT). NORRBOTTENS LÄN: Lulea, *Caspary* (IA). **Switzerland:** ST. GALLEN CANTON: Bei Au, 1858, *Herb. P. Zollikofer* (NY). **Syria:** Prope Damascum (Esh-Sham) ad frontes Barrada Copiose, 4000 ped. elev., 1855, *T. Kotschy 90* (G, P). **U.S.S.R.** KASAKHISTAN: Near Uralsk, 1925, *T. Pojarkova 348* (S). MOLDAVSKAJA: Delta Danube (Bessarabica), *N. Zelenetsky* (G). NOVGOROD: County of Starorussa, *I. Normanskoy* (MIN). SIBIR: Tomsk, 1933, *L. Sergievskaja* (NY).

1a. *N. luteum* subsp. *luteum* × *N. luteum* subsp. *pumilum* (Map 4)

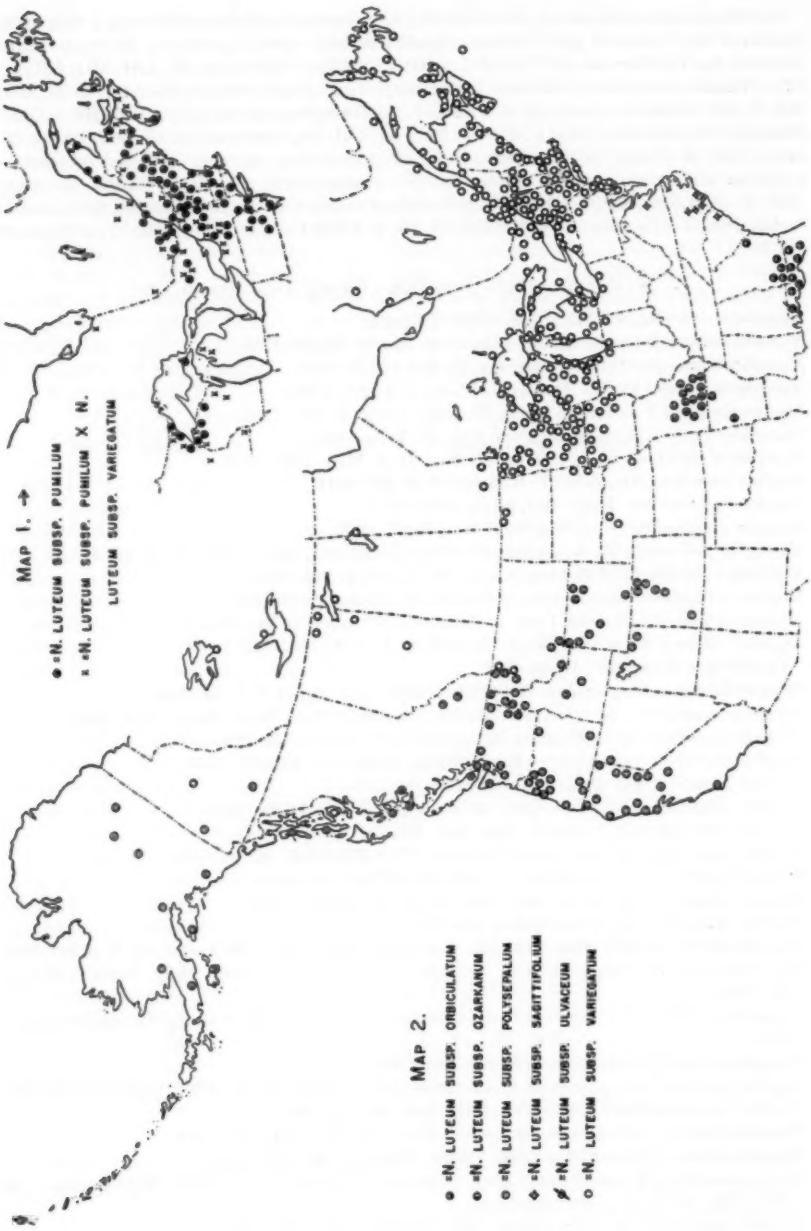
Nuphar minimum β *spennerianum* Gaudin, Fl. Helv. **3:** 439. 1828.
Nuphar intermedium Ledeb. Fl. Alt. **2:** 274. 1830.
"*Nyphar intermedium* Ledeb." Walp. Rep. Bot. Syst. **1:** 108. 1842.
Nuphar rivulare Dum. Bull. Soc. Roy. Bot. Belg. **3:** 5–6. 1864.
Nuphar luteum × *pumilum* var. *medium* Casp. Abh. Nat. Ges. Halle, **11:** 181–270. 1870.
Nuphar luteum × *pumilum* var. *polypetalum* Casp. *ibid.*
Nuphar luteum × *pumilum* var. *sublutea* Casp. *ibid.*
Nuphar affine Harz, Botan. Centralbl. **53:** 227. 1893.
Nuphar pumilum β *spennerianum* (Gaudin) Rouy & Foucaud, Fl. Fr. **1:** 150. 1893.
Nuphar juranum Magnin, Rev. Gen. Bot. **5:** 257. 1893. (*Nomen nudum*; the description supplied in Ann. Soc. Bot. Lyon, **19:** 5. 1894.)
Nuphar intermedium f. *chlorocephalum* Roemer, Allg. Bot. Zeit. **13:** 168. 1907.
Nuphar intermedium f. *luteocephalum* Roemer, *ibid.*
Nymphaea affinis (Harz) Hayek, Fl. Steierm. p. 437. 1908.
× *Nymphaea intermedia* (Ledeb.) Schuster, Bull. Herb. Boiss. ser. 2. **8:** 70. 1908.
× *Nymphaea intermedia* var. *hirtella* Schuster, *ibid.*
× *Nymphaea intermedia* var. *media* (Casp.) Schuster, *ibid.*
× *Nymphaea intermedia* var. *polypetala* (Casp.) Schuster, *ibid.*
× *Nymphaea intermedia* var. *sublutea* (Casp.) Schuster, *ibid.*
Nymphaea lutea var. *affinis* (Harz) Schuster, Bull. Herb. Boiss. ser. 2. **8:** 69. 1908.
Nuphar luteum × *N. pumilum* var. *chlorocephalum* (Römer) Hegi, Ills. Fl. Mitt.-Europ. **3:** 448. 1912.
Nymphozanthus affinis (Harz) Fern. Rhodora, **21:** 188. 1919.
Nymphozanthus intermedius (Ledeb.) Fern. Rhodora, **21:** 187. 1919.
Nymphozanthus juranus (Magnin) Fern. Rhodora, **21:** 188. 1919.
Nuphar pumilum × *luteum* f. *submersum* Glück *in* Pascher, Die Susswasser-Flora Mitteleuropas, **15:** 256. 1936. (Without Latin diagnosis).
Nuphar pumilum × *luteum* f. *terrestre* Glück, *ibid.* (Without Latin diagnosis).

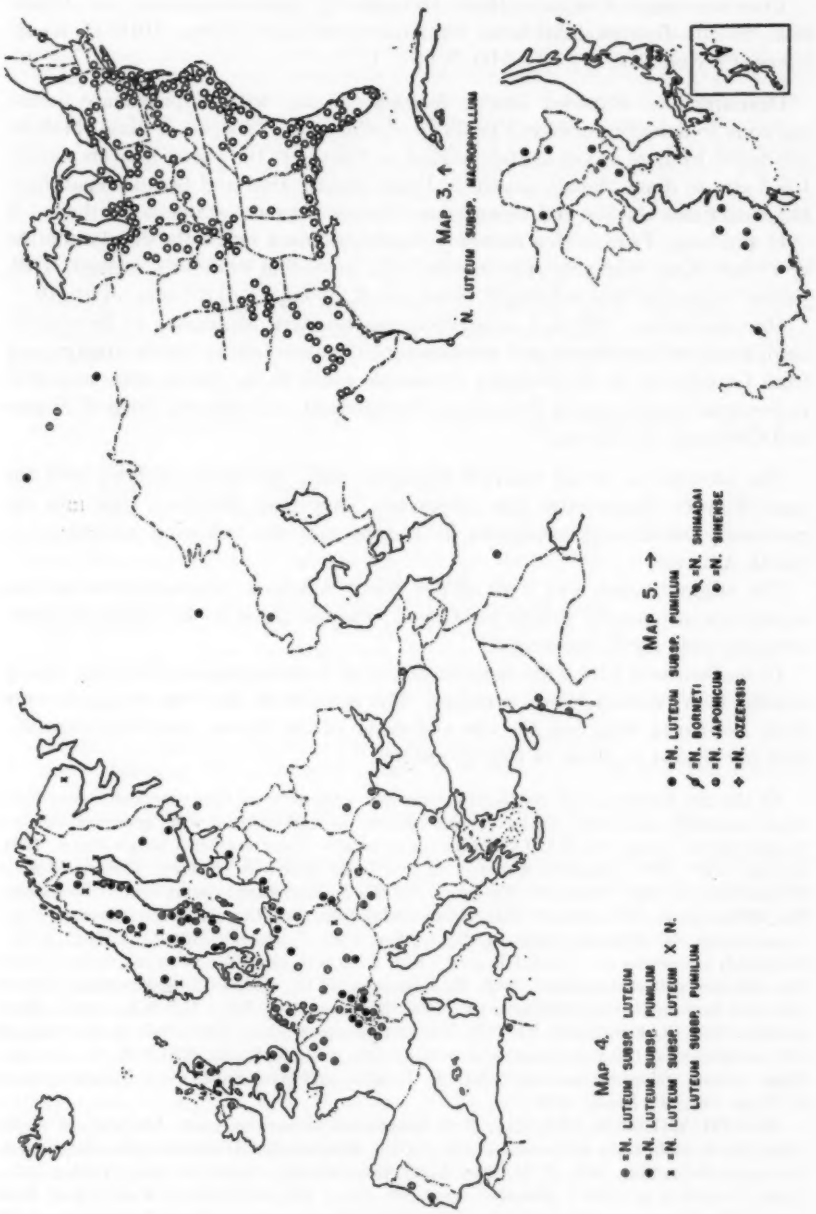
Owing to general usage this category has been retained for those plants intermediate between the two taxa involved. These plants, the pollen of which is reported to be as much as eighty-five per cent sterile, are often found in the vicinity of the supposed ancestors but may exist by themselves.

Of 122 specimens examined, the following have been selected as exhibiting a wide geographical and morphological range: **Czechoslovakia:** MORAVIA OCCID., in aquis stagnantibus pr. Volfířov, ad urb. Dačice, ca 560 m., 1927, *J. Macku 214* (G, GH, MO, MT, P, US). **Finland:** LAPIN LÄÄNI: Muonio, in flumine jexta templum, 1915, *J. Montell 1169* (G, MO, NY, P, UC). **France:** VOSGES: *Herb. Fauche 7* (G). **Germany:** OBERBAYERN, 1897, *Harz* (GH). **Poland:** Collatzer-See, 1912, *F. Roemer 5410* (G, GH, S). **Scotland:** Small loch near Aviemore, 1894, *H. Groves* (S). **Sweden:** JÄMPLAND LÄN: In lacu calcareo (Lillsjön) Odensalae, 4 chilom. ab Östersund, 1914, *G. Ohrstedt* (S). NORRBOTTENS LÄN: Karl Gustav, Karungi, 1928, *H. Svenonius 804* (G, GH, MT). **Switzerland:** FRIBOURG CANTON: Lac de Châtel-Saint-Denis, 1896, *Fr. Cavillier & Burnat 583* (G, P). **U.S.S.R.:** KOLA: Ponoj, 1863, *N. Fellman 15* (G, P).

2. *N. luteum* subsp. *pumilum* (Timm) Beal, comb. nov.

Nymphaea lutea L. Sp. Pl. p. 510. 1753. (In part.)
Nymphaea lutea β pumila Timm, Mag. Nat. Meckl. **2**: 250. 1795.
Nymphaea lutea β minima Willd. Sp. Pl. **2**(2): 1151. 1799.
Nymphaea pumila Hoffm. Deutschl. Fl. ed. 2. **1**: 241. 1800.
Nymphaea lutea β kalmiana Mich. Fl. Bor.-Amer. **1**: 311. 1803.
Nymphaea lutea • microphylla Pers. Syn. Pl. **2**: 63. 1807.
Nymphaea kalmiana Sims, *in* Curtis's Bot. Mag. **31**: t. 1243. 1810.
Nuphar kalmiana Ait. f. Hort. Kew. ed. 2. **3**: 295. 1811.
Nuphar minima Sm. Engl. Bot. **32**: t. 2292. 1811.
Nuphar pumila DC. Reg. Veg. Sys. Nat. **2**: 61. 1821.
Nenuphar minimum Link, Enum. Pl. Hort. Reg. Bot. Berol. Pars 2, p. 70. 1822.
Nenuphar pumila Bluff & Fing. Comp. Fl. Germ. **1**: 705. 1825.
Nuphar minimum β spennerianum Gaudin, Fl. Helv. **3**: 439. 1828.
Nuphar luteum β kalmiana Torr. & Gray, Fl. N. Amer. p. 38. 1838.
Nyphar luteum β kalmianum Walp. Rep. Bot. Syst. **1**: 108. 1842.
"*Nyphar pumilum* Sm." Walp. *ibid.*
Nuphar luteum var. *pumilum* Gray, Man. Bot. N. U.S. ed 5, p. 57. 1868.
"*Nuphar pumilum* var. *rehsteineri* Burnat" Gremli, Neue Beitr. Schw. **1**: 2. 1880.
Nuphar pumilum var. *glabratum* Harz, Botan. Centralbl. **53**: 229. 1893.
Nuphar pumilum var. *hookerii* Harz, Botan. Centralbl. **53**: 228. 1893.
Nuphar pumilum var. *timmii* Harz, *ibid.*
Nuphar pumilum α pumilum Rouy & Foucaud, Fl. Fr. **1**: 150. 1893.
Nuphar centricavatum Schuster, Allg. Bot. Zeit. p. 145. 1905.
Nuphar pumilum var. *genuinum* Schuster, Allg. Bot. Zeit, **12**: 80. 1906.
Nuphar pumilum var. *genuinum* f. *glabratum* (Harz) Schuster, *ibid.*
Nuphar pumilum var. *genuinum* f. *sericotrichum* Schuster, *ibid.*
Nuphar pumilum var. *stellatifidum* Schuster, *ibid.*
Nymphaea microphylla (Pers.) Robins. & Fernald, Gray's New Man. Bot. ed. 7, p. 391. 1908.
Nymphaea pumila var. *genuina* f. *glabrata* (Harz) Schuster, Bull. Herb. Boiss. ser. 2. **8**: 70. 1908.
Nymphaea pumila var. *genuina* f. *sericotricha* sf. *rehsteineri* (Burnat ap. Gremli) Schuster, *ibid.*
Nymphaea pumila var. *stellatifida* Schuster, *ibid.*
Nuphar pumilum var. *genuinum* f. *glabratum* (Harz) Hegi, Ills. Fl. Mitt.-Europ. **3**: 448. 1912.
Nuphar microphyllum (Pers.) Fern. Rhodora, **19**: 111. 1917.
Nymphozanthus centricavatus (Schuster) Fern. Rhodora, **21**: 188. 1919.
Nymphozanthus microphyllus (Pers.) Fern. Rhodora, **21**: 186. 1919.
Nuphar pumilum f. *submersum* Glück *in* Pascher, Die Susswasser-Flora Mitteleuropas, **15**: 254. 1936 (Without Latin diagnosis).
Nuphar pumilum f. *terrestre* Glück, *ibid.* (Without Latin diagnosis).
Nuphar microphyllum f. *multisepalum* O. Lakela, Rhodora, **58**: 76. 1956.


MAP 1. →
● =N. LUTEUM SUBSP. PUMILUM
x =N. LUTEUM SUBSP. PUMILUM X N. LUTEUM SUBSP. VARIEGATUM
MAP 2.
● =N. LUTEUM SUBSP. ORBICULATUM
● =N. LUTEUM SUBSP. OZARKANUM
○ =N. LUTEUM SUBSP. POLYSEPALUM
◆ =N. LUTEUM SUBSP. SAGITTIFOLIUM
✗ =N. LUTEUM SUBSP. ULVACEUM
○ =N. LUTEUM SUBSP. VARIEGATUM


MAP 3. ↑
N. LUTEUM SUBSP. MACROPHYLLUM
MAP 4.
● =N. LUTEUM SUBSP. LUTEUM
● =N. LUTEUM SUBSP. PUMILUM
× =N. LUTEUM SUBSP. LUTEUM × N. LUTEUM SUBSP. PUMILUM
MAP 5. →
● =N. LUTEUM SUBSP. PUMILUM
=N. BORNETI
=N. JAPONICUM
=N. OZEENSIS
=N. SHIMADAI
=N. SINENSE

TYPE SPECIMEN: *Neotype* in Herb. Delessert (G). Savonia borealis, par. Maaninka, in sinu Juurikkalahti lacus Pöljänjärvi, in fundo limosa, 1918, *O. Kyyhkynen, Pl. Fin. Exs. 1170* (G, MO, NY, P, UC).

DESCRIPTION.—Exposed leaves floating, ovate, with approximate lobes; glabrous to densely pubescent below; sometimes only 2.5 cm. in diam. Petioles sub-terete to more or less acutely angled, at least near the blade. Flowers mostly 1.5–3 cm. in diam. Sepals mostly 5. Petals mostly thin and broadly spatulate, but sometimes thicker and emarginate; shorter than the stamens. Anthers 1–2 (–3) mm. long. Fruit with a narrowly constricted neck below the deeply dentate or crenate disk. Stigmatic rays mostly 5–14, extending to the disk margin. Disk yellow to more or less red-tinged. Seeds small, ovoid, up to 3.5 mm. in length.

DISTRIBUTION.—(Maps 1, 4, 5) From northeastern Minnesota to Newfoundland, south to New Jersey and southeastern Pennsylvania in North America and from Lapland to the Kamtsjatka Peninsula, south to the Baltic areas and local in Scotland, southwestern Poland and Switzerland and adjacent areas of France and Germany, in Eurasia.

The crenate to deeply-toothed stigmatic disk, the short anthers, and the small flowers, characterize this subspecies. They may, however, pass into the previously mentioned subspecies in Europe and the following subspecies in North America.

The stigmatic disk and fruit of the North American representatives of this subspecies are usually deeply red-tinged, whereas those of the Eurasian specimens are only rarely red-tinged.

In southeastern China the representatives of *Nuphar* appear to be very closely related to *N. luteum* subsp. *pumilum*. The anthers of the Chinese plants vary from 2.5–4 mm. long, but the size and shape of the flowers, fruit and stigmatic disk are similar to those of this subspecies.

Of the 274 Eurasian and 368 North American specimens of this subspecies that have been examined, the following have been selected as exhibiting a wide geographical and morphological range: EURASIA: **China:** MANCHURIA: Near station Chingis-Kahn, 1903, *Litvinov 3407* (NY). **Finland:** KUOPION LÄÄNI: Type Specimen. **France:** VOSGES: Moselle à Remiremont, 1848, *Mathieu et Tocquaine 313* (G, P). **Germany:** OBERBAYERN: Wesslinger See, 588 m. elev., 1905, *Eigner, Schuster & Vollman Fl. Exs. Bav. 927* (GH). **Norway:** Gudbrandsdalen (G). **Poland:** Polzin, Collatzer-See, 1913, *F. Roemer 5408* (G, GH, S, TEX). **Scotland:** ABERDEEN CO.: Loch Kinnord, 1879, *E. Lomax 49* (NY). **Sweden:** NORRBOTTENS LÄN: In lacu prope Munksund, 1906, *H. Johansson* (MIN, RM, UC). **Switzerland:** ZURICH CANTON: Lac de Hütten, 660 m. elev., 1866, *E. Burnat* (G, NY). **U.S.S.R.** AMUR: Amur medius, 1891, *S. Korshinsky* (G, GH, US). BASJKIRIJA: (Gub. Ufa) 1887, *S. Korzchinsky* (G). KAMCHATKA: Bolsheretsk, 20 km. to the south, 1921, *E. Hultén 2890* (GH, S). LATVIJA: Rīga, in lacu "Kupferhamersee," 1900, *K. Kupffer 1053* (G). SIBIR: Prov. Tomsk in valle fl. Tym, 1904, *P. Krylov* (GH).

NORTH AMERICA-CANADA. **New Brunswick:** CARLETON DIST.: Ox-bow cut of St. John River, 1945, *Dare & Gorham 45-907* (NCU). **Newfoundland:** Southeastern Newfoundland near Salmonier, 1932, *A. M. Ayre* (GH). **Nova Scotia:** YARMOUTH DIST.: Tusket Lake, 1920, *Fernald et al.* (GH). **Ontario:** NIPISSING DIST.: Algonquin Prov. Park, Otter Slide Lake, 1900, *Macoun 21,699* (GH, MO, NY, US). **Quebec:** LABELLE DIST.: Nomininge, 1929, *E. Roy 1673* (RM). TERREBONNE DIST.: Riviere-du-Nord, 1920, *Fr. Marie-Victorin* (F, MT, RM, US).

U. S. A. **Connecticut:** NEW HAVEN CO.: Pond in Housatonic River meadow, 1895, *E. H. Eames* (GH, MIN, NY, US). **Maine:** AROOSTOCK CO.: Shallow pond, St. Francis, 1893, *Fernald 10* (GH, MICH, MIN, MO, NY, US). OXFORD CO.: Gilead, 1903, *A. H. Moore 1119* (MICH, UC). **Massachusetts:** BERKSHIRE CO.: Shallow lagoon, Housatonic River, Sheffield, 1920, *J. R. Churchill* (MO, NCSC, US). **Michigan:** LUCE CO.: Clark Lake, T.49N., R. 8W., Sect. 24, 1952, *R. McVaugh 12755* (MICH). **Minnesota:** SAINT LOUIS CO.: "Narrows" of Elbow Lake on road to Crone Lake, 1941, *O. Lakela 4547* (MIN, NY, WIS). **New Hampshire:** COOS CO.: 2nd Conn. Lake, 1904, *A. Doolittle 113*, (US). **New Jersey:** PASSAIC CO.: Pompton Lake, 1892, *T. Morong* (NY). **New York:** CLINTON CO.: Plattsburg, 1885, *T. Morong* (GH). CORTLAND CO.: Willow Grove Mill Pond, Truxton, 1916, *K. M. Wiegand 6430* (CU, F, GH, MICH, MO, NCSC, TEX). SAINT LAWRENCE CO.: Bay W. of Lonesome Bay, Black Lake, 1931, *Muenscher & Maguire 2253* (CU, F, MO). **Pennsylvania:** MONROE CO.: Head of Naomi Pines, 1904, *J. W. Harshberger* (F, GH, MIN, MO, RM, US). **Vermont:** CALEDONIA CO.: Joe's Pond, Danville, 1894, *Burbank, Grout & Eggleston* (GH, NY). **Wisconsin:** DOUGLAS CO.: Amnicon Lake, 1927, *L. R. Wilson 333* (MIN, WIS). SAWYER CO.: Mucky shore of Lost Land Lake, T.42 N., R.6 W., Sect. 32., Hayward, 1929, *Fassett & Gilbert 12349* (GH, MO, WIS).

2a. *N. luteum* subsp. *pumilum* × *N. luteum* subsp. *variegatum* (Map 1)

Nuphar lutea Pursh, Fl. Amer. Sept. ed. 2. **2:** 369. 1816.
Nyphar luteum Walp. Rep. Bot. Syst. **1:** 108. 1842.
Nuphar advena var. *hybrida* Peck, Ann. Rpt. N. Y. St. Mus. Nat. Hist. no. 127, p. 53. 1881.
"*Nuphar luteum* var. ————(?) Fletcher's Fl. Ott." Macoun, Cat. Can. Pl. **1:** 32–33. 1883.
Nuphar advena Ait. var. (?) *minor* Morong, Bot. Gaz. **11:** 167. 1886.
Nuphar rubrodiscum Morong, Bot. Gaz. **11:** 167–168. 1886.
Nymphaea rubrodisca Greene, Bull. Torrey Bot. Club, **15:** 84. 1888.
"*Nymphaea fletcheri* ×" Lawson, Trans. Roy. Soc. Can. **6:** 119. 1888.
Nuphar advena var. *minus* (Morong) Wats. & Coult. Gray's Man. ed. 6, p. 56. 1889.
Nymphaea hybrida Peck, Bull. N. Y. St. Mus. **6:** 75. 1899.
"× ? *Nymphaea rubrodisca* (Morong) Greene" Robins. & Fern. Gray's New Man. Bot. ed. 7. p. 391. 1908.
Nymphozanthus rubrodiscus (Morong) Fern. Rhodora, **21:** 187. 1919.
Nuphar × *hybridum* (Peck) Bergmans, Vaste Pl. Rotsheet, ed. 2, p. 548. 1939. (*Non-viso, fide* Kew.)
"× *Nuphar rubrodiscum* Morong" Fern. Gray's Man. Bot. ed. 8, p. 639. 1950.

Owing to general usage this category has been retained for those plants intermediate between the two taxa involved. The plants may be found in the vicinity of the supposed ancestors but may be found by themselves. These intermediate plants are reported to be sterile in some areas and completely fertile in others.

Of 326 specimens examined, the following have been selected as exhibiting a wide geographical and morphological range: CANADA. **New Brunswick:** WESTMORELAND DIST.: Creek flowing into Morice Lake, Sackville, 1947, *W. G. Dore 45-1039* (F, MIN). **Newfoundland:** Grand Falls, shallow pools in bogs, *Fernald & Wiegand 5417* (F, GH, S, US). **Nova Scotia:** DIGBY DIST.: Hectanooga Lake, 1920, *C. H. Bissell et al. 21220* (GH). PICTOU DIST.: Millpond near Pictou, 1901, *C. D. Howe & W. F. Lang 610* (GH, NY). **Ontario:** RENFREW DIST.: Cross Lake, Bonne Chere Mts., 1899. *L. M. Umbach* (GH, MIN, US, WIS). MOOSE RIVER BASIN, 1903, *J. Bell* (GH). **Quebec:** GASPE DIST.: Grand Etang: décharge du lac, 1928, *J. Rousseau 31203* (GH, MT). QUEBEC-MONTMORENCY DIST.: Quebec, 1902, *W. W. Eggleston 3010* (CU, GH, MIN, MO, NY, S). ISLAND OF ANTICOSTI: Lac a la Croix, 1927, *Fr. Marie-Victorin & Fr. Rolland-Germain 27285* (F, GH, MO, S).

U. S. A. **Maine:** AROOSTOCK CO.: Birch Brook, n. end of Cross Lake, Eagle Lake Chain, 1903, *W. C. Kendall* (US). PENOBSCOT CO.: Chemo Stream, Bradley, 1905, *O. W. Knight*

(ILL, RM). **Massachusetts:** MIDDLESEX CO.: Concord River, Concord, 1894, *J. R. Churchill* (MO). **Michigan:** CHEBOYGAN CO.: Lloyd Pool, Hook Point, North Fishtail Bay, Douglas Lake, 1952, *F. K. Sparrow* (MICH). **Minnesota:** COOK CO.: Pond near Brule River, 1924, *F. K. Butters & C. O. Rosendahl 4525* (GH, MIN, NY). **New Hampshire:** CHESHIRE CO.: Gilmore Pond, 1897, *B. L. Robinson 263* (GH). **New Jersey:** CAMDEN CO.: South Branch of Pensauken Creek n. of Park Avenue Bridge, Pensauken, 1926, *Adams & Trudell 384* (GH). **New York:** WAYNE CO.: S. end of Blind Sodus Bay, Wolcott Twp., 1939, *Clausen & Hinkey 4436* (CU, NY). **Pennsylvania:** MONROE CO.: 1893, *N. L. Britton* (NY, US). **Vermont:** ADDISON CO.: Ferrisburg, 1901, *W. W. Eggleston 2543* (ILL, MIN, MO, NY). CALEDONIA CO.: Joe's Pond, Danville, 1894, *Burbank, Grout & Eggleston* (GH, MICH, NY). **Wisconsin:** DOUGLAS CO.: West Superior, 1902, *C. Ballard* (US). SHAWANO CO.: Shawano Lake, Washington Twp., 1931, *Hotchkiss & Koehler 4308* (MIN, US).

3. *N. luteum* subsp. *variegatum* (Engelm. *ex* Clinton) Beal, comb. nov.

Nymphaea advena Ait. Hort. Kew. **2:** 226–227. 1789. (In part).
Nuphar advena Ait. f. Hort. Kew. ed. 2. **3:** 295. 1811. (In part).
Nenuphar advena Link, Enum. Pl. Hort. Reg. Bot. Berol. **2:** 70. 1822. (In part).
Nuphar americana Provancher, Fl. Canad. **1:** 28–29. 1862. (In part).
Nuphar variegatum Engelm. *ex* Clinton, 19th Ann. Rept. of Regents of the Univ. of State of N. Y. p. 73. 1866.
Nuphar advena var. *variegatum* (Engelm.) Gray, Man. Bot. N. U. S. ed. 5, p. 57. 1868.
Nymphaea variegata (Engelm.) Miller, Proc. Biol. Soc. Wash. **15:** 11–13. 1902.
Nymphaea advena var. *variegata* (Engelm.) Fern. Rhodora, **10:** 49. 1908.
Nymphaea americana (Provancher) Miller & Standley, Contrib. U. S. Nat. Herb. **16:** 78–82. 1912.
Nymphaea fraterna Miller & Standley, Contrib. U. S. Nat. Herb. **16:** 82. 1912.
Nymphozanthus variegatus (Engelm.) Fern. var. *lutescens* Farwell, Amer. Mid. Nat. **8:** 270. 1923.
"*Nymphaea advena* Soland." House, N. Y. State Mus. Bull. No. 254, p. 329. 1924.
Nuphar fraternum (Miller & Standley) Standley, Field Mus. Pub. Nat. Hist. Bot. Ser. **8:** 310. 1931.
Nuphar advena subsp. *variegatum* (Engelm.) Clausen, Cornell Univ. Agri. Exp. Sta. Mem. 291, pp. 7–8. 1949.

The first published reference to *variegatum* as a specific epithet was made by "one of the regents" of the University of the State of New York, in 1866. The author, who has been identified as G. W. Clinton, wrote: "In reference to this species [*Nuphar variegatum* Engelm.], the venerable E. Durand, under the date of March 10, 1866, writes me: '*Nuphar variegatum* I found in Philadelphia, in Dr. Short's Herb., now in Acad. of Nat. Sci. a specimen marked New York, from H. H. Eaton's Herb.' it 'is easily distinguished from *N. advena*, by its leaves always floating, with closed sinuses and winged petioles.' I have just been informed, authentically, that Dr. Englemann now doubts the distinctness of this species."

TYPE SPECIMEN: *Lectotype* (GH). Grand Marais, mouth of Connors Creek, Detroit, July 23, 1865, *Bigelow*.

This specimen is accompanied by a letter from Dr. Engelmann to Dr. Gray (dated Dec. 28, 1865) in which Dr. Engelmann writes: "I do not hesitate to put it [a red-flowered *Nuphar* previously sent to Dr. Engelmann by Dr. Gray] together with Bigelow's coloured *Nuphar* as a new species: *Nuphar variegatum*."

Numerous specimens, collected by Bigelow in the vicinity of Detroit, are extant in the Gray Herbarium and the Herbarium of the Missouri Botanical Garden. Some of these collections are referred to *N. luteum* subsp. *variegatum*, others to *N. luteum* subsp. *macrophyllum*, and others appear to be intermediate between these taxa.

DESCRIPTION.—Exposed leaves usually floating, oblong to ovate, with approximate or overlapping lobes; glabrous below. Petiole conspicuously flattened and winged. Sepals usually 6; mostly red-tinged within. Anthers 3–8 mm. long. Fruit slightly constricted below the entire to more or less crenate stigmatic disk; often red-tinged. Stigmatic rays mostly 7–16 (–26) often extending to the margin. Seeds ovoid, up to 5 mm. long.

DISTRIBUTION.—(Map 2) From the Yukon Territory and the Great Bear Lake to Newfoundland, south to western Montana, Nebraska, Iowa, northern Illinois, northern Ohio and Delaware. (Specimens collected by F. L. Howey in northwestern Arkansas in 1883 (UARK) and by C. W. Short in Kentucky in 1940 (NY) may represent range extensions of this subspecies or perhaps only incorrect collection data.)

The conspicuously winged petiole and six red-tinged sepals distinguish this subspecies throughout most of its range. These characteristics, however, pass into *N. luteum* subsp. *pumilum* in the region from Lake Superior to New England and adjacent Canada, and into *N. luteum* subsp. *macrophyllum* where the ranges of the two overlap.

The *Nymphaea fraterna* of Miller & Standley and the *Nymphozanthus variegatum* var. *lutescens* of Farwell are no more than minor forms of this subspecies which are perhaps partially intermediate with the following subspecies.

Of 1011 specimens examined, the following have been selected as exhibiting a wide geographical and morphological range: CANADA. **Alberta:** VICTORIA DIST.: Eastern edge of Lily Lake, 23 mi. n. w. of Fort Saskatchewan, 1945, *G. H. Turner 4546* (S). WOOD BUFFALO PARK: Shore of Lake, about 59°36′ N., 113°7′ W., 1929, *H. M. Raup 2349* (GH, NY, UC, US). **Mackenzie:** Small lake s.e. of Cross Fault Lake, McTavish Arm, Great Bear Lake, 1948, *H. T. Shacklette 2933* (MICH, US). Yellowknife, 62°27′ N., 114°22′ W., rooted in ooze of small lake by old townsite, 1949, *W. J. Cody & J. B. McCanse 2675* (MO, MT, NCSC, S). **Manitoba:** Ashland, 1886, *Herb T. Morong* (NY). **New Brunswick:** YORK DIST.: Fredericton, 1880, *J. Fowler* (MO). **Newfoundland:** Trinity Bay, Old Perlican, 1914, *G. S. Torrey 19* (GH). **Nova Scotia:** GUYSBOROUGH DIST.: Canso, 1901, *J. Fowler* (GH, MO, US, WIS). CAPE BRETON ISLAND: Valley of the Banasois River, 1915, *G. E. Nichols 1226* (GH). SABLE ISLAND: Fresh water of Left Hand Pond, 1913, *H. St. John 1233* (GH, NY, US). **Ontario:** KENT DIST.: St. Lukes Bay, Lake St. Clair, 1948, *Soper & Dale 4071* (MT, US). NIPISSING DIST.: Algonquin Prov. Park, Cache Lake, 1900, *Macoun 21697* (MO, NY, US). THUNDER BAY DIST.: Vicinity of Peninsula about Lat. 48°45′ N., Long. 86°15′ W., 1939, *Taylor, Bannan & Harrison 1207* (S). **Quebec:** JAMES BAY REGION: Petit lac Hill Portage, 56° N±, 75°20′ W., 1945, *Rev. A. Dutilly & Rev. E. Lepage 14331* (WIS). SAGUENAY DIST.: Seven Islands, 1907, *C. B. Robinson 889* (NY). MAGDALEN ISLANDS: Etangs près du Cap-de-l'Est, Ile da la Grande-Entrée, 1919, *F. Marie-Victorin & F. Rolland-Germain* (GH, MT). **Saskatchewan:** Small lake about 2 mi. w. of Ennuyeuse Creek, about 59°3′ N., 109°34′ W., 1935. *H. M. Raup 7000* (GH, NY, S). **Yukon:** Lake about 3 mi. n. e. of Mayo, 63°36′ N., 135°53′ W., 1949, *J. A. Calder & J. M. Gillett 4056* (MO, MT, RM, US).

U. S. A. **Arkansas:** Northwest Arkansas: Ponds, 1883, *F. L. Howey*, (UARK). **Connecti-**

cut: NEW HAVEN CO.: Stagnant water, New Haven, 1884, *W. E. Safford* (US). **Delaware:** SUSSEX CO.: Record's Pond, Laurel, 1927, *J. M. Fogg, Jr. 1828* (GH). **Illinois:** LAKE CO.: Cedar Lake, 1942, *G. N. Jones 17687* (ILL). **Indiana:** NOBLE CO.: W. side of Bear Lake, 1930, *C. C. Deam 49392* (GH). **Iowa:** CERRO GORDO CO.: W. end of Clear Lake, Ventura, 1933, *B. Shimek* (IA, MIN, WIS). DICKINSON CO.: S. end of Lower Gar Lake, 1916, *B. Shimek* (IA, ILL, MIN, MO, US). MUSCATINE CO.: Along Cedar River, 1891, *F. Reppert* (IA). **Kentucky:** No locality given, 1940, *C. W. Short* (NY). **Maine:** AROOSTOCK CO.: Pettiquaggamas Lake, 1893, *M. L. Fernald 9* (F, GH, MO, NY, UC, US). KNOX CO.: Sawyers near Camp Medomak, 1929, *J. A. Steyermark* (F). **Massachusetts:** HAMPDEN CO.: Springfield, 1910, *F. Knot* (GH, ILL, MIN, NY, US). **Michigan:** ALLEGAN CO.: W. end of Swan Lake, 1902. *W. F. Wight 5* (NY, US). KEWEENAW CO.: Isle Royale Nat. Park, Hidden Lake, 1942, *H. & V. Bailey 4271* (MICH). WASTENAW CO.: Whitmore Lake, 1901, *T. G. Williamson* (MICH), **Minnesota:** BENTON CO.: Mayhen Creek, 1939, *J. B. Moyle* (MIN). CASS CO.: Lake Kilpatrick, 1893, *C. A. Ballard* (GH, MIN, RM, S, UC, US, WIS). COOK CO.: Pond near Brule River, 1924, *Rosendahl & Butters 4524* (MIN). ROCK CO.: Creek, Mound Springs State Park, 1946, *Moore & Huff 18693* (MIN). ROSEAU CO.: Creek at Badger, 1939, *Moore 12243* (MIN). **Montana:** FLATHEAD CO.: Big Fork, 1904, *W. W. Jones* (UC, US). **Nebraska:** CASS CO.: Greenwood, 1200 ft. elev., 1890, *T. A. Williams 322* (US). GRANT CO.: 30 mi. s. of Whitman in Swan Lake, 1893, *P. A. Rydberg 1650* (GH). **New Hampshire:** HILLSBOROUGH CO.: Pond, Pelham, 1930 (RM). **New Jersey:** ATLANTIC CO.: Mays Landing, 1927, *J. M. Fogg, Jr. 2184* (DUKE, F, GH). CUMBERLAND CO.: Marl-pit, junction of Sarah & Horse Runs, 3.75 mi. n. w. of Shiloh, 1927, *J. W. Adams 843* (GH, MO). OCEAN CO.: Toms River, Aug. 6, 1903, *M. W. Lyon* (US). **New York:** CHAUTAUQUA CO.: Slough hole, Stockton, 1914, *O. P. Phelps 444* (GH). CLINTON CO.: Upper Chateaugay Lake, 1930, *Muenscher & Maguire 1157* (CU, GH). SARATOGA CO.: Marsh, n. w. corner of Saratoga Lake, 1932, *W. C. Muenscher & A. A. Lindsey 3305* (CU, UC). SCHUYLER CO.: Cayuta Lake, 1927, *W. C. Muenscher 16958* (CU). **North Dakota:** BOTTINEAU CO.: Turtle Mts., Roland Twp., 1917, *F. P. Metcalf 518* (US). RANSOM CO.: Enderlin, 1911, *H. F. Bergman 908* (F). **Ohio:** ERIE CO.: Sandusky, 1902, *W. A. Kellerman* (US). **Pennsylvania:** MONROE CO.: Naomi Pines, 1893, *N. L. Britton* (NY). **Rhode Island:** NEWPORT CO.: Between Pilot Hill & Southeast Point, Block Island, 1913, *Fernald et al. 9502* (GH). **South Dakota:** BROOKINGS CO.: White, 1893, *Thornber* (MO, UC, US). **Vermont:** ORLEANS CO.: Willoughby, 1892, *H. H. Rusby* (MICH, NY, UC). **Wisconsin:** BAYFIELD CO.: Port Wing, lagoon, 1929, *N. C. Fassett 12340* (WIS). BROWN CO.: Green Bay, 1903, *J. H. Shutte* (US). WASHINGTON CO.: Oconomowoc River, Richfield, 1929, *B. Ruandt* (WIS).

4. *N. luteum* subsp. *macrophyllum* (Small) Beal, comb. nov.

Nymphaea lutea sensu Walt. Fl. Carol. p. 154–155. 1788.
Nymphaea advena Ait. Hort. Kew. **2:** 226–227. 1789. (In part).
Nymphaea advena Ait. *sensu* Michx. Fl. Bor. Amer. **1:** 311. 1803.
Nymphaea arifolia Salisb. *in* Konig & Sims Ann. Bot. **2:** 71. 1806.
Nuphar advena Ait. f. Hort. Kew. ed. 2. **3:** 295. 1811. (In part).
Nuphar advena Ait. f. *sensu* Pursh, Fl. Amer. Sept. ed. 2. **2:** 369. 1816.
Nenuphar advena (Ait.) Link, Enum. Pl. Hort. Reg. Bot. Berol. **2:** 70. 1822. (In part).
Nuphar advena β tomentosa Nutt. *ex* Torr. & Gray, Fl. N. Amer. p. 58. 1838.
"*Nyphar advena* Ait." Walp. Rep. Bot. Syst. **1:** 108. 1842.
"*Nyphar advena β tomentosum*" Walp. *ibid.*
Nuphar americana Provancher, Fl. Canad. **1:** 28–29. 1862. (In part).
Nymphaea macrophylla Small, Bull. Torrey Bot. Club **25:** 465–466. 1898.
Nymphaea fluviatilis Harper, Bull. Torrey Bot. Club **33:** 234. 1906.
Nymphaea advena subsp. *erythraea* Miller & Standley, Contrib. U. S. Nat. Herb. **16:** 91. 1912.
Nymphaea advena subsp. *macrophylla* (Small) Miller & Standley, Contrib. U. S. Nat. Herb. **16:** 89–90. 1912.
Nymphaea chartacea Miller & Standley, Contrib. U. S. Nat. Herb. **16:** 94–95. 1912.

Nymphaea ludoviciana Miller & Standley, Contrib. U. S. Nat. Herb. **16:** 92–93. 1912.
Nymphaea microcarpa Miller & Standley, Contrib. U. S. Nat. Herb. **16:** 100–101. 1912.
Nymphaea ovata Miller & Standley, Contrib. U. S. Nat. Herb. **16:** 97–99. 1912.
Nymphaea puberula Miller & Standley, Contrib. U. S. Nat. Herb. **16:** 99–100. 1912.
"*Nymphona advena* (Soland.)" Nieuw. Amer. Mid. Nat. **3:** 295. 1914.
Nymphozanthus advena (Ait.) Fern. Rhodora, **21:** 186. 1919.
Nymphozanthus advena var. *macrophyllus* (Small) Fern. *ibid.*
Nymphozanthus fluviatilis (Harper) Fern. Rhodora, **21:** 188. 1919.
"*Nymphaea advena* Soland." House, N. Y. State Mus. Bull. No. 254, p. 329. 1924. (In part).
Nuphar advena var. *brevifolia* Standley, Rhodora, **31:** 37. 1929.
Nuphar advena var. *erythraeum* (Miller & Standley) Standley, Field Mus. Nat. Hist. Bot. Ser. **8:** 310–311. 1931.
Nuphar chartaceum (Miller & Standley) Standley, *ibid.*
Nuphar fluviatile (Harper) Standley, *ibid.*
Nuphar ludovicianum (Miller & Standley) Standley, *ibid.*
Nuphar microcarpum (Miller & Standley) Standley, *ibid.*
Nuphar ovatum (Miller & Standley) Standley, *ibid.*
Nuphar puberulum (Miller & Standley) Standley, *ibid.*
× *Nuphar interfluitans* Fern. Rhodora, **44:** 397–398. 1942.
Nuphar advena var. *cubana* León, Riv. Soc. Cub. Bot. **4:** 9. 1947.
Nuphar advena (Sol.) R. Br. subsp. *typicum* Clausen, Cornell Univ. Agri. Exp. Sta. Mem. 291, pp. 7–8, 1949.
Nuphar puteorum Fern. Rhodora, **52:** 65–67. 1950.

TYPE SPECIMEN: *Holotype* (NY). Vicinity of Eustis, Lake Co., Florida, Aug. 16–24, 1894, *G. V. Nash 1751* (F, GH, MICH, MIN, MO, NY, US).

DESCRIPTION.—Exposed leaves floating or erect, ovate, with overlapping to divergent lobes; glabrous to more or less pubescent below. Submersed leaves, when present, thin and translucent, essentially like the floating ones in size and shape. Petioles terete to more or less flattened above; glabrous to pubescent. Sepals 6, rarely red-tinged. Petals thick, truncate to emarginate. Anthers 3–7 mm. long., sometimes red-tinged. Fruit slightly constricted below the entire to crenate stigmatic disk. Stigmatic rays 5–18 (–23), mostly ending 1–2 mm. from the disk margin. Stigmatic disk sometimes red-tinged. Seeds numerous, 3.5–5 mm. wide and 4–6 mm. long.

DISTRIBUTION.—(Map 3) Southern Wisconsin to southern Maine and south to northeastern Mexico and Cuba.

This subspecies is extremely variable, exhibiting typically erect and glabrous leaves in the northern part of its range, where it passes into *N. luteum* subsp. *variegatum*. In the Carolinas it passes into *N. luteum* subsp. *sagittifolium* of tidal rivers. In neutral or slightly acidic ponds and streams of South Carolina, Georgia and northern Florida, where its leaves are typically floating and more or less pubescent below, it passes into *N. luteum* subsp. *orbiculatum*. In central and southern Florida and in Cuba, its leaves are again typically emersed, glabrous and with divergent lobes. The stigmatic disk of these plants in Florida and Cuba is often red-tinged and the seeds are large, approaching the limit of the range in this character. In western Florida, southern Alabama, southern Mississippi and adjacent Louisiana it passes into *N. luteum* subsp. *ulvaceum* of the Blackwater

River. The plants in Texas exhibit great variability in leaf size, shape, and degree of pubescence. In the Ozark region of Missouri and adjacent Arkansas it passes into *N. luteum* subsp. *ozarkanum*. In North Carolina, colonies have been observed in which the inner surface of the sepals is deeply red-tinged. Throughout most of its range, however, this subspecies is characterized by its terete to more or less flattened petioles, ovate leaves with divergent lobes and yellow-green sepals.

Of 878 specimens examined, the following exhibited characteristics passing into closely related subspecies in areas of range overlap and adjacent regions: *N. luteum* subsp. *variegatum*, 42; *N. luteum* subsp. *sagittifolium*, 44; *N. luteum* subsp. *ulvaceum*, 25; *N. luteum* subsp. *ozarkanum*, 10; *N. luteum* subsp. *orbiculatum*, 72.

The following have been selected as exhibiting a wide geographical and morphological range: CANADA: **Ontario:** WELLAND DIST.: Riviere Welland, 1931, *F. Marie-Victorin, F. Rolland-Germain & E. Jacques 49253* (GH, MT).

CUBA. PINAR DEL RIO: Small stream, Guane to Mantua, 1911, *J. A. Shafer 11213* (NY, US).

MEXICO. **Coahuila:** Muzquiz, 1935, *E. Marsh 18* (TEX). **Tamaulipas:** Altamira, 1898, *E. A. Goldman 95* (US).

U. S. A. **Alabama:** MOBILE CO.: 1885, *C. Mohr* (US). WINSTON CO.: Lewis Creek, 1897 *H. Eggert* (MO). **Arkansas:** PIKE CO.: Antoine River, 1932, *D. Demaree 9666* (GH, MO, NY). SCOTT CO.: Creek, Waldron, 1938, *Fassett & Watts 19747* (F, GH, MO, NY). **Connecticut:** LITCHFIELD CO.: Lagoon bordering Blackberry River, North Canaan, 1916, *E. B. Harger 6698* (UC). **Delaware:** SUSSEX CO.: Fresh tidal mud, Nanticoke River, 0.75 mi. s. w. of Seaford, 1938, *E. C. Earle 1807* (WIS). **District of Columbia:** Marsh, Mt. Hamilton Tract, 1923, *E. C. Leonard 5454* (US). **Florida:** DUVAL CO.: Creek near Jacksonville, 1901, *A. H. Curtiss 6844* (GH, ILL, MIN, MO, NY, S, SMU, UC, US). ESCAMBIA CO.: Cypress swamp along Escambia River 4 mi. e. of Cottage Hill, 1941, *R. Brinker 500* (MO). GULF CO.: Dead Lakes, 1.5 mi. n. of Wewahitchka, 1952, *E. O. Beal 321* (IA). LEE CO.: Cypress Swamp, vicinity of Fort Myers, 1916, *P. C. Standley 12632* (US). WASHINGTON CO.: Choctawhatchee River at Fla. Hwy. 79, 1952, *E. O. Beal 318* (IA). **Georgia:** BRYAN CO.: Shallow lagoons of Canoochee River near Groveland, 1903, *R. M. Harper 1849* (F, GH, MO, NY, US). EARLY CO.: Porter Pond w. of Cedar Springs, 1949, *R. F. Thorne & W. C. Muenscher 9234a* (GA, IA). LOWNDES CO.: Long Pond, 1902, *R. M. Harper 1611* (MO, NY, US). **Illinois:** FULTON CO.: Rice Lake, 9 mi. s. e. of Canton, 1949, *R. J. Miller* (ILL). MCHENRY CO.: Algonquin, 1878, *W. A. Nason* (ILL). MACON CO.: 1897, *I. W. Clokey 26* (UC). RICHLAND CO.: Near mouth of Big Creek, 1928, *R. Ridgeway 3351* (F). WABASH CO.: Little Bompas Creek on Lancaster-West Salem road, 1953, *E. O. Beal 354* (IA). WILL CO.: Stream at New Lennox, 1911, *E. E. Sherff* (F). **Indiana:** LAWRENCE CO.: Beaver Creek, ½ mi. n. of Huron, 1934, *R. M. Kriebel 1647* (DUKE). STEUBEN CO.: Inlet of Lake Gage, 1903, *C. C. Deam* (NY). **Kansas:** CHAUTAUQUA CO.: 1896, *A. S. Hitchcock 607* (GH, MO, NY, RM, US). **Kentucky:** BALLARD CO.: Swan Pond, 1915, *C. P. Alexander 292* (US). BATH CO.: Ditches near Midland, 1941, *E. L. Braun 4363* (GH). **Louisiana:** CALCASIEU PAR.: Vicinity of Lake Charles, 1904, *A. A. Allison 219* (US). SAINT TAMMANY PAR.: N. Shore of Lake Ponchartrain, 1903, *R. S. Cocks* (US). **Maine:** SAGADAHOC CO.: Tidal flats of Kennebec River below Richmond, 1948, *Fassett 27872* (MIN, MO, WIS). **Maryland:** ANNE ARUNDEL CO.: Muddy bank of Patuxent River, Hills Bridge, 1950, *L. B. Smith 5039* (US). **Michigan:** KENT CO.: Grand Rapids, 1892, *H. M. Bailey* (MICH). **Mississippi:** HARRISON CO.: Biloxi, 1898, *S. M. Tracy 5012* (US). **Missouri:** JEFFERSON CO.: De Soto, 1887, *H. E. Hasse* (NY). SHANNON CO.: Folk Pond, T. 27 N., R. 3 W., Sect. 31, 3 mi. s. of Winona, 1936, *J. A. Steyermark 12210* (MO). VERNON CO.: Maus Lake, 2 mi. s. of Prairie City, 1938, *J. A. Steyermark 9841* (F, MO). **New Jersey:** BERGEN CO.: Closta, 1909, *N. Taylor 472* (NY). **New York:** CHAUTAUQUA CO.: Findley Lake, 1937, *R. McVaugh & O. F. Curtis, Jr.*

(CU). GENESEE CO.: In lateral stream of Black Creek, Bergen Swamp, 1946, *W. C. Muenscher 22114* (CU). ULSTER CO.: Tidal mud-flat, Hudson River, Saugerities, 1941, *W. C. Muenscher 20388* (CU, S). LONG ISLAND: Flanders, 1928, *W. C. Ferguson 7023* (NY). **North Carolina:** HENDERSON CO.: Small run 1 mi. from Fletcher on Co. road to Cogsdill Limestone Co., 1949, *A. E. Radford 4853* (NCU). SAMPSON CO.: Coharie Swamp on U. S. 421, 1949, *E. T. Browne, Jr.* (NCU). TYRRELL CO.: Ditch 7 mi. n. of Fairfield, 1938. *T. E. Kerr & R. K. Godfrey 3922* (GH, NCSC, US). **Ohio:** ERIE CO.: Chapelle Creek, Florence Twp., 1919, *E. L. Moseley* (MO, US). HARRISON CO.: Cadiz Junction, 1902, *W. A. Kellerman 3882* (US). LOGAN CO.: Pond near Lewistown, 1934, *E. C. Leonard 17258* (US). **Oklahoma:** CHOCTAW CO.: Ponds near Ft. Toroson, 1916, *H. W. Houghton 3997* (GH, MO, NY). MCCURTAIN CO.: Mountain Fork River, Eagletown, 1936, *J. de Gruchy 73* (MO, NY). **Pennsylvania:** CRAWFORD CO.: Marshy pond, 2 mi. s. s. w. of Cochranton, 1947, *H. A. Wahl 5158* (FLAS). LANCASTER CO.: Blue Lake, 3 mi. e. of Cocalico, 1948, *N. C. Fassett 27864* (GH, WIS). **South Carolina:** BERKELEY CO.: Santee Canal, n. w. of Bonneau, 1939, *Godfrey & Tryon, Jr. 489* (GH, MO, NY, UC, US). CHARLESTON CO.: Roadside Ponds, US 17, 0.5 mi. e. of Edisto River, 1950, *Wilbur & Webster 2847* (MICH). SPARTANBURG CO.: Oxbow pond on Motlow Creek, Campobello, 1942, *E. H. Walker 3515* (NCU, US). **Tennessee:** CARROLL CO.: Margin of stream, Hollow Rock Jc., 1922, *H. K. Svenson 429* (GH). **Texas:** BELL CO.: Salado Springs, 1932, *S. E. Wolff 3452* (S). BEXAR CO.: San Antonio, 1911, *J. Clemens 793* (MO, RM). COMAL CO.: New Braunfels, 1910, *Otto Locke* (US). DALLAS CO.: Turtle Creek s. of Beverly Drive, 1954, *L. H. Shinners 19242* (SMU). HARRIS CO.: Houston, 3 mi. s. at Bray's Bayou, 1912, *G. L. Fisher 94* (US). HAYS CO.: San Marcos, 1897, *Trelease* (MO). MCLENNAN CO.: Slough n. of bridge over S. Bosque River fork of Lake Waco, w. of Waco along Hwy. 6, 1946, *C. L. York 46231* (F, ILL, TEX). VAL VERDE CO.: Still pools, Devils River, 1917, *E. J. Palmer 12362* (GH, MO, NY, UC, US). **Vermont:** BENNINGTON CO.: Pownal, 1853, *G. L. Ames* (MICH). **Virginia:** FAIRFAX CO.: Creek in pasture near Holmes Run Road, Falls Church, 1945, *Fassett 22341* (US, WIS). NEW KENT CO.: Deep fresh tidal water of Chickahominy River s. E. of Windsor Shades, 1941, *Fernald & Long 13607* (GA, GH, MO, SMU, US). NORFOLK CO.: Smith's Pond, 1903, *G. S. Miller, Jr.* (US). ROANOKE CO.: Sand spit, Roanoke River 0.8 mi. s. s. w. of Salem P. O., 1941, *C. E. Wood, Jr. 1256* (UC). WARREN CO.: Passage Creek, 1897, *G. S. Miller* (US). **West Virginia:** JACKSON CO.: Ravenswood, 1930, *W. Va. U. Bot. Exped.* (MIN). POCAHONTAS CO.: Stream, Minnahaha Springs, 1930, *E. E. Berkley 1379* (MO). **Wisconsin:** COLUMBIA CO.: Long Lake, Wisconsin River bottom opposite Portage, 1946, *N. C. Fassett 27404* (WIS). JEFFERSON CO.: Shallow stream, Palmyra, 1943, *N. C. Fassett 22082* (MT, NY, WIS). WALWORTH CO.: Edge of Whitewater Lake, Sect. 34, Town of Whitewater, 1938, *Wadmond & Fassett* (MIN).

5. *N. luteum* subsp. *sagittifolium* (Walt.) Beal, comb. nov.

Nymphaea sagittifolia Walt. Fl. Carol. p. 155. 1788.
Nymphaea longifolia Michx. Fl. Bor. Amer. **1:** 312. 1803.
Nymphaea sagittaefolia Salisb. *in* Konig & Sims Ann. Bot. **2:** 71. 1806.
Nymphaea sagittata Pers. Syn. Pl. **2:** 63. 1807.
Nuphar sagittaefolia Pursh, Fl. Amer. Sept. ed. 2. **2:** 370. 1816.
Nuphar longifolium Smith *in* Rees's Cycl. No. 5. 1819.
Ropalon sagittatum Raf. New Fl. N. Amer. **2:** 17. 1836. (Part 2 is reported to have been published in the second half of 1837 by J. H. Barnhart, Torreya **7:** 177–181. 1907.)
"*Nymphaea hastata* Michx." Steud. Nom. Bot. ed. 2. **2:** 200. 1841.
Nymphozanthus sagittifolius (Walt.) Fern. Rhodora, **21:** 186. 1919.
Nuphar sagittifolium (Walt.) Pursh, of Gleason's New B. & B. Ills. Fl. **2:** 150. 1952.

TYPE SPECIMEN: *Neotype* (NY). Oriente Carolina Septentrionalis, July 1885, *G. McCarthy*.

DESCRIPTION.—Exposed leaves floating, glabrous, lanceolate to linear, three

to five times as long as wide; lobes usually not overlapping, the sinus less than one-fourth the length of the blade. Submersed leaves numerous, thin and translucent, essentially like the floating in size and shape. Stigmatic rays linear to elliptical.

DISTRIBUTION.—(Map 2) Tidal reaches of rivers in Virginia, North Carolina (one collection also from "Statesville," Iredell Co., N. C.) and South Carolina.

This subspecies (as *Nymphaea sagittifolia*) has been reported to occur in Alabama (Mohr, 1901). Deam (1940) reports it, upon the authority of Schneck, to have occurred in the Lower Wabash Valley. All the specimens examined from these areas have been *N. luteum* subsp. *macrophyllum* and it is very doubtful if the above-mentioned reports refer to anything but variants of that subspecies.

A specimen consisting of only one leaf, collected by J. M. Greenman (No. 4825) in pool, Morris Farm, Bristol," Bucks Co., Pennsylvania (MO), appears to be of this subspecies. Although it is not so indicated, the plant was most probably cultivated in this location.

Specimens collected by M. E. Hymans, Statesville (Iredell Co.), N. C. (MIN, MO, NY) are considerably distant from the normal Coastal Plain habitat and the existence of this subspecies in Iredell Col. N. C. needs confirmation.

The elongate leaves and shallow sinus are the most conspicuous features of this subspecies. In this regard it may be compared with *N. luteum* subsp. *ulvaceum* of the Blackwater River. The leaves of the latter are shorter, being only about two and one-half times as long as wide and the lobes are usually overlapping. Moreover, the number of sepals in the Blackwater River plants varies from six to nine and the stigmatic rays are more or less elliptical, as compared with the six sepals and usually linear stigmatic rays of *N. luteum* subsp. *sagittifolium*.

Of 80 specimens examined, the following have been selected as typifying the subspecies. **North Carolina:** COLUMBUS CO.: Sturgeon Creek near U. S. 74-76, 1949, *A. E. Radford 4349* (NCU). NEW HANOVER CO.: Creek in Wilmington, 1923, *J. R. Churchill* (GH, MO, NCSC). **South Carolina:** GEORGETOWN CO.: Marsh, Black River, 10 mi. n. of Georgetown, 1939, *R. K. Godfrey & R. M. Tryon, Jr., 1086* (GH, MO, NY, UC, US). **Virginia:** CHARLES CITY CO.: Deep fresh tidal water of Chickahominy River near Cypress Bank Landing, 1941, *M. L. Fernald & B. Long 15334* (GH, MO, SMU, TEX, US).

6. *N. luteum* subsp. *ulvaceum* (Miller & Standley) Beal, comb. nov.

Nymphaea ulvacea Miller & Standley, Contrib. U. S. Nat. Herb. **16**: 97. 1912.
Nuphar ulvaceum (Miller & Standley) Standley, Field Mus. Nat. Hist. Bot. Ser. **8**: 310–311. 1931.

TYPE SPECIMEN: *Holotype* (US, No. 357366). Blackwater River near Milton, Florida, May 14, 1898, *A. H. Curtiss 6409* (F, GH, ILL, MO, NY, SMU, UC, US).

DESCRIPTION.—Exposed leaves floating, glabrous, lanceolate, about two and one-half times as long as wide; lobes usually overlapping, the sinus less than one-fourth the length of the blade. Submersed leaves numerous, thin and translucent, essentially like the floating leaves in size and shape. Sepals six to nine. Stigmatic rays usually elliptical.

DISTRIBUTION.—(Map 2) In the Blackwater River of western Florida.

This taxon appears to be very closely related to those forms of *N. luteum* subsp. *macrophyllum* that are intermediate with the preceding subspecies.

Additional specimen examined. **Florida:** SANTA ROSA CO.: Blackwater River, Fish Hatchery near Holts, 1952, *E. O. Beal 315* (IA).

7. *N. luteum* subsp. *ozarkanum* (Miller & Standley) Beal, comb. nov.

Nymphaea ozarkana Miller & Standley, Contrib. U. S. Nat. Herb. **16:** 91–92. 1912.
Nuphar ozarkanum (Miller & Standley) Standley, Field Mus. Nat. Hist. Bot. Ser. **8:** 310–311. 1931.
Nymphozanthus ozarkanus (Miller & Standley) Palmer & Steyermark, Ann. Missouri Bot. Gard. **22:** 538. 1935.

TYPE SPECIMEN: *Holotype* (US, No. 615581). Along the White River in southern Missouri, Aug. 1910, *O. M. Smith.*

DESCRIPTION.—Exposed leaves usually floating, oblong-ovate to orbicular, with approximate lobes. Petioles terete. Sepals six, more or less red-tinged within. Fruit variously red-tinged. Seeds few, 15–48 per fruit and large, 3.5–5.2 mm. wide and 5–6 mm. long.

DISTRIBUTION.—(Map 2) Ozark region of Missouri and local in northwestern Arkansas.

The characteristic features of these plants are not restricted to this taxon for it closely resembles *N. luteum* subsp. *macrophyllum* and *N. luteum* subsp. *variegatum*, being distinguished from the former by its red-tinged sepals and fruit, and from the latter by the terete petioles. The shape of leaves, presence of red pigmentation and seed numbers barely distinguish this subspecies from the highly variable *N. luteum* subsp. *macrophyllum* and subspecific recognition is questionable.

Sterile specimens, apparently of *N. luteum* subsp. *pumilum*, were found by Deam "In a pond about 5 miles northwest of Graysville," Sullivan Co., Indiana in June, 1918 (US). On the label Deam notes: "This form was found in a small colony in an opening among *Nymphaea advena* [*Nuphar luteum* subsp. *macrophyllum*]. This species was common and almost took up the area of the pond that was under water. The leaves of this specimen were floating, while those of *N. advena* were erect. I take this to be some species different from *N. advena*, although I could not find any flowers, etc." Whether these plants were merely depauperate specimens of *N. luteum* subsp. *macrophyllum*, genetically reconstituted *N. luteum* subsp. *pumilum*, or remnants of previous glacial influence, is not known. It is not inconceivable, however, that the red-tinged sepals and fruit of *N. luteum* subsp. *ozarkanum* may have resulted from previous contact with the more northern *N. luteum* subsp. *pumilum*.

Of 60 specimens examined, the following have been selected as typifying the subspecies. **Arkansas:** BAXTER CO.: Sloughs, Cotter, 1914, *E. J. Palmer 6018* (F, MO). SCOTT CO.: Big Fourche River near slough bridge, Boles, 1938, *Fassett & Watts 19748* (GH). **Missouri:** BENTON CO.: Shallow water of Beech Branch tributary to Deer Creek, 1.25 mi. e. of Edwards,

1938, *J. A. Steyermark 7262* (F). CRAWFORD CO.: Courtois Creek, T.38N., R.2W., Sect. 19–20, 1–1.5 mi. w. of Butts Post Office, 1941, *Steyermark 41305* (F). DALLAS CO.: Niangua River, 1.5 mi. n. of Corkery, 1934, *Steyermark 13870* (MO, US). GREENE CO.: Edge of the James, vicinity of Gates, 1912, *P. C. Standley 9380* (US). LACLEDE CO.: Slough paralleling Osage Fork near Pease Mill, 1936, *Steyermark 10541* (F, MO). OZARK CO.: Millpond at Hammond, 1937, *Steyermark 22807* (F, MO). PULASKI CO.: Big Piney River s. of Miller Spring, 2 mi. n. e. of Big Piney, 1937, *Steyermark 25538* (F, MO). RIPLEY CO.: Sloughs along West Fork of Current River near Ponder, 1933, *Palmer & Steyermark 41641* (GH, MO, NY). SHANNON CO.: Jack's Fork, Rymer's Ranch, 1953, *E. O. Beal 369* (IA). WAYNE CO.: Lost Creek, T.27N., R.7E., Sect. 8, 2.5 mi. s. of Shook Post Office, 1938, *Steyermark 6551* (F, MO).

8. *N. luteum* subsp. *orbiculatum* (Small) Beal, comb. nov.

Nymphaea orbiculata Small, Bull. Torrey Bot. Club **23:** 128. 1896.
Nymphaea bombycina Miller & Standley, Contrib. U. S. Nat. Herb. **16:** 102–103. 1912.
Nymphozanthus bombycinus (Miller & Standley) Fern. Rhodora, **21:** 188. 1919.
Nuphar bombycinum (Miller & Standley) Standley, Field Mus. Nat. Hist. Bot. Ser. **8:** 310–311. 1931.
Nuphar orbiculatum (Small) Standley, *ibid.*

TYPE SPECIMEN: *Lectotype* (NY). Along or near the Ochlocknee River near Thomasville, July 12–22, 1895, *J. K. Small* (F, NY). Small notes the type locality as: "Collected in a small lake near Thomasville, southern Georgia."

DESCRIPTION.—Leaves floating, orbicular to broadly ovate, thick and leathery, with broadly rounded, approximate to overlapping lobes; densely pubescent below. Petioles and peduncles pubescent. Fruit very slightly constricted below the entire to irregularly crenate stigmatic disk; large, often 5 cm. in diameter. Stigmatic disk green, yellow or sometimes red-tinged, the rays 12–28 in number.

DISTRIBUTION.—(Map 2) Acidic ponds of the Coastal Plain in Georgia and northern Florida.

The densely pubescent, thick leaves, pubescent petioles and peduncles and the robust nature of the plants characterize this subspecies. It is difficult, however, to distinguish between this and the representatives of *N. luteum* subsp. *macrophyllum* in adjacent areas.

Specimens of this subspecies, when cultivated in the State University of Iowa Greenhouses, were remarkably glabrous, indicating that at least the pubescent nature of this subspecies may be directly influenced by its environment.

Of 59 specimens examined, the following have been selected as typifying the subspecies. **Florida:** BAY CO.: Small pond near Lake Merial on Fla. Hwy. 77, n. of Panama City, 1952, *Beal 319* (IA). GILCHRIST CO.: Ditch along Fla. Hwy. 26, w. of Newberry, 1952, *Beal 335* (IA). HAMILTON CO.: Pond (possibly Lake Octahatchee) w. of Jennings, 1952, *Beal 331* (IA). SUWANNEE CO.: Pond near Wellborn, 1901, *Curtiss 6900* (GH, ILL, MIN, MO, NY, S, UC, US). WASHINGTON CO.: Six mi. s. of Wausau, 1950, *Webster & Wilbur 3621* (MICH). **Georgia:** DECATUR CO.: Cane Water Pond, 1952, *Beal 293* (IA). EARLY CO.: Porter Pond, w. of Cedar Springs, 1949, *Thorne & Muenscher 9234* (F, GA). LOWNDES CO.: Five mi. s. e. of Valdosta, 1950, *Wilbur & Webster 2689* (MICH). MILLER CO.: East side of Babcock's Pond, 1952, *Beal 306* (IA). SCREVEN CO.: Boggy, open limesink pond, 1940, *D. E. Eyles 7591* (NCSC). SEMINOLE CO.: Ray's Lake, 1949, *Thorne & Muenscher 9120* (IA).

9. *N. luteum* subsp. *polysepalum* (Engelm.) Beal, comb. nov.

Nuphar polysepalum Engelm. Trans. St. Louis Acad. Sci., Proc. **2**: 283–285. 1865.
Nuphar polysepalum var. *pictum* Engelm. *ibid.*
Nymphaea polysepala Green, Bull. Torrey Bot. Club, **15**: 84. 1888.
Nymphozanthus polysepalus (Engelm.) Fern. Rhodora, **21**: 187. 1919.

TYPE SPECIMEN: *Lectotype* (MO, No. 2494, excluding folder). Osborn's Lake, 1864, *C. C. Parry* (GH, MO).

Engelmann notes that the specimens collected by Dr. Parry ". . . have been largely used in the. . . description" and that in 1860, "Dr. F. V. Hayden collected it . . . in a small lake between Henry's Fork and Snake Fork of the Columbia River, at an altitude of 6,500 feet." He also notes that "Miss Merrill, in the year 1862, brought from Gibson's Lake, near Long's Peak [Colorado] some of the large reddish sepals. . . ." Osborn's Lake is ". . .in the same region [as Gibson's Lake], at an altitude of 8,800 feet. . . ."

DESCRIPTION.—Leaves usually floating, sometimes emersed; broadly ovate to oblong, glabrous; the lobes rounded to acute, divergent to overlapping. Petioles terete. Flowers as large as 12 cm. in diameter when fully open. Sepals 7–9 (–12). Petals usually yellow but sometimes red-tinged. Stamens with yellow to deeply red-tinged anthers, the filament often extending 1–4 mm. beyond the anther. Stigmatic disk entire to deeply crenate, usually deeply umbilicate; the rays 9–36, usually 20–25. Seeds narrowly ovoid, 2.5–3.2 mm. wide and 3.5–5 mm. long.

DISTRIBUTION.—(MAP 2) Alaska southward along the Pacific Coast and Sierra Nevada range to San Luis Obispo Co. in California, and southeastward in the Rocky Moutains to northeastern Utah and Colorado.

The floating leaves, large flowers, numerous sepals, red-tinged anthers with conspicuous connective extensions and small, narrowly ovate seeds characterize this subspecies. These features, however, are by no means consistent. In the Pacific coastal areas especially, this subspecies approaches the habit of *N. luteum* subsp. *macrophyllum*, and in northwestern Montana it approaches the habit of *N. luteum* subsp. *variegatum*.

Of 518 specimens examined, the following exhibit a wide geographical and morphological range. ALASKA. **First Judicial Div.:** Marshy edge of Klawak Lake, Prince of Wales Isl., 1915, *E. P. Walker 992* (F, GH, MO, NY, RM, UC, US). **Third Judicial Div.:** Anchorage area, 1943, *C. L. York 186* (F, TEX); Attu Isl., pond, 100 ft. elev., 1945, *R. M. Hardey 250* (MIN). **Fourth Judicial Div.:** Fairbanks, 1927, *L. J. Palmer 1802* (US).

CANADA. **British Columbia:** KOOTENAY DIST.: Swamp by Goldstream, about 118°20′ W., 51°40′ N., 1905, *C. H. Shaw 986* (GH, MIN, MO, NY). VANCOUVER ISLAND DIST.: San Juan Lake & River, 1902, *C. O. Rosendahl 893* (MIN, MO, NY, RM). **Yucon:** Canal Road: Mile 36–42, along w. bank of Nisutlin River, 2750 ft. elev., 1944, *Porsild & Breitung 10803* (US). White Pass: 1914, *A. Eastwood 916* (GH).

U. S. A. **California:** BUTTE CO.: Jonesville, 1700 m. elev., 1930, *E. B. Copeland 415* (F, GH, MICH, MIN, MO, NY, RM, S, UC, US, WIS). EL DORADO CO.: Lily Lake near Fallen Leaf, 1933, *I. L. Wiggins 6756* (GH, RM, UC). LASSEN CO.: Pond near Lake Almanor, 1929, *D. Tebbe 132* (UC). MARIN CO.: Lagunitas, 1877, *Edward* (NY). PLACER CO.: Above Emigrant Gap, Crystal Lake, 1910, *H. M. Hall 8738* (UC, US). PLUMAS CO.: Snake Lake Valley, 4000 ft. elev., 1912, *H. M. Hall 9304* (UC, US). SAN LUIS OBISPO CO.: Between Oceano & Callender,

1929, *R. S. Ferris 8028* (F, GH, NY, UC). **Colorado:** BOULDER CO.: Ward, 2700 ft. elev., 1933, *H. Lenander* (S). LAKE CO.: Near Leadville, *L. M. & N. T. Sehedin* (RM). SAN JUAN CO.: 20 mi. s. of Silvertown, 1936, *Goodman & Payson 2779* (NY). SUMMIT CO.: Gibson's Lake about 40 mi. n. w. of Denver toward Long's Peak, 1862, *Merrill* (MO) [this specimen, labeled as "*Nuphar picta* nov. sp." by C. C. Parry in 1864, is in a folder on same sheet as the lectotype]. **Idaho:** BLAINE CO.: Quiet places in Malad River near Corral, 1916, *Macbride & Payson 2908* (GH, MO, RM, UC, US). KOOTENAI CO.: Ponds, Valley of Lake Tesemini, 1892, *Sandberg et al. 701* (F, GH, NY, US). COEUR D'ALENE MOUNTAINS: Old Mission Peak, 670 m. elev., *Leiberg 1412* (F, GH, MIN, NY, RM, UC). **Montana:** FLATHEAD CO.: Big Fork, 1908, *J. Clemens* (GH). GALLATIN CO.: Ponds, Spanish Basin, 1898, *J. W. Blankinship* (MO). YELLOWSTONE NATIONAL PARK: Obsidion Cliff, 1900, *W. W. Jones* (UC). **Nevada:** WASHOE CO.: About Marlette Lake, 2460 m. elev., 1902, *Baker 1479* (GH, MO, NY, UC, US). **Oregon:** COOS CO.: Near Coos Bay, 1880, *Engelmann* (MO). CLACKMANS CO.: Mt. Hood, moist meadow, 1898, *Applegate 2844* (US). HARNEY CO.: Shallow water of Lily Lake, Steens Mountains, 1946, *Maguire et al. 26749* (NY). MULTNOMAH CO.: Vicinity of Portland, 1905, *Palmer 1474* (F, MO, NY, US). UMATILLA CO.: Alpine pond, Blue Mts. 1888, *W. C. Cusick 1525* (GH). **Utah:** SUMMIT CO.: Shallow pond in Spruce forest, Uintah Mts., 10000 ft. elev., 1926, *Payson 5124* (GH, MO, NY, RM, S, UC, US). **Washington:** KING CO.: Lake Union, 1898, *Savage et al.* (F, IA, MO). SAN JUAN CO.: Lake Tucker, San Juan Islands, 1917, *Zeller 979* (GH, MIN, MO, NY, US). STEVENS CO.: Loon Lake, 1903, *Beattie et al. 2078* (MT, UC, US). WHITMAN CO.: Union Flat Creek, 1892, *Hull* (MIN, NY). **Wyoming:** SHERIDAN CO.: Willits Creek, 1909, *V. Willits 360* (RM). SUBLETTE CO.: Lake, head of Green River, 1894, *A. Nelson 898* (GH, ILL, MIN, MO, NY, RM, US). TETON CO.: Shallow water near Leighs Lake, 1901, *Merrill & Wilcox 1116* (GH, NY, RM, US). YELLOWSTONE NATIONAL PARK: Small lake, Norris Geyser Basin, 1899, *A. & E. Nelson 6152* (GH, ILL, MIN, MO, NY, RM, US).

EXCLUDED TAXA

Only 56 specimens of *Nuphar* from China and Japan have been examined (Map 5). Of these, 43 fall within *N. japonicum* DC., the synonymy of which, as presented below, was proposed by Beal (1955) and substantiated by Makino (1955).

Nymphaea lutea sensu Thunberg, Fl. Jap. p. 223. 1784. *non* L.
Nuphar japonicum DC. var. *crenatum* subvar. *luteum* Casp, *in* Miquel, Ann. Mus. Bot. Ludg.-Bat. II. t. 8. p. 254. 1866. (printed also as subvar. *flava* on page 255.)
Nuphar japonicum DC. var. *crenatum* subvar. *rubrotinctum* Casp. *ibid.*
Nuphar japonicum DC. var. *subintegerrimum* Casp. *ibid.*
Nymphaea japonica (DC.) O. K. Rev. Gen. Pl. **1:** 12. 1891.
Nuphar subintegerrimum (Casp.) Makino, Bot. Mag. Tokyo, **24:** 141–142. 1910. [spelled *N. subintegerimum* by Makino (1955)].
Nuphar subintegerrimum f. *rubrotinctum* (Casp.) Makino, *ibid.*
Nymphozanthus japonicus (DC.) Fern. Rhodora, **21:** 187. 1919.
Nymphozanthus subintegerrimus (Casp.) Fern. *ibid.*

An examination of 13 specimens of the following taxa has shown that the plants differ from *N. luteum* subsp. *pumilum*, especially in anther length (2.5–4 mm.) and leaf texture, but otherwise appear to be closely related to that taxon.

Nuphar borneti Léve. & Van. Soc. Bot. Fr. **51:** cxliii. 1904. Kouy-Tcheou: Tsin-gai and environs de Gan-pin. Kweichow: *J. Cavalerie 3034* (P), *1160 & 7850* (K); *Y. Tsiang 7422* (GH, S), *8615* (NY).
Nuphar ozeensis Miki, Studies of Historical and Natural Monuments in Kyotohu, **18:** 1937. (*Non-viso.*) Gumma: Ozegahara (*ca.* 1400 m.), 1946. *S. Suzuki* (GH).

Nuphar shimadai Hayata, Ic. Pl. Formos. **6:** 2. 1916. Shiuchikucho: Shimpo. Formosa, Shimpo: *Y. Shimada* (UC).

Nuphar sinense Hand. Mzt. Anz. Akad. Wiss. Wien, Math.-nat. **63:** 8. 1926. Hunan: Tschangscha. Chekiang: *Y. L. Keng 570* (UC). Kiangsi: *S. K. Lau 4349* (G, GH, S, US). Kwangtung: *Tsang Wai Tak & Wong Kam Chow* (UC).

No specimens of the following taxa have been examined:

Nuphar japonica var. *stenophyllum* Miki, Studies of Historical and Natural Monuments in Kyotohu, **18:** 1937. (*Non viso*).

Nuphar oguraensis Miki, Bot. Mag. Tokyo, **48:** 334–335. 1934. Hondo: Prov. Yamashiro, Mukojima; Prov. Kawachi; Prov. Hizen, the Tatara River; Prov. Satsuma.

Nuphar subintegerinum Mak. *in* Miki, Oekol. Stud. Sumpf. u. Wasserg. Ogura-teiche (1927) 143. (*Non viso*). = *N. oguraensis fide* S. Miki, Bot. Mag. Tokyo, **48:** 334–335. 1934.

Nuphar subpumilum Miki, Studies of Historical and Natural Monuments in Kyotohu, **18:** 1937. (*Non viso*).

DISCUSSION

GROWTH HABIT.—The stems are rhizomatous and although occasionally found exposed to the atmosphere, are usually buried in mud or submerged in as much as ten feet of water. Laing (1941) reported that the stem tips of *Nuphar advenum* (*N. luteum* subsp. *macrophyllum*) grow best when the oxygen concentration is 0–1 per cent, less rapidly at a concentration of 1.5 per cent, and not at all in concentrations above three per cent. He found the optimum water depth for stem tip growth in this taxon to be four to six feet.

The rhizomes branch freely. Older portions of the rhizome decay, leaving only the younger tips to bear leaves and flowers. By repeated branching and isolation of the branch tips through decay, ever-increasing numbers of individual plants are produced. Thus an entire colony may be clonal in nature and mass collections must be made with care. Such a growth habit should, however, prove highly valuable in determining the effect of environmental control since rhizome branches of identical genetic composition may be easily used in transplant studies.

POLLINATING AGENTS.—The flowers of *Nuphar* are proterogynous, with the anthers dehiscing centripetally over a period of several days. Pollinating agents are reported by Robertson (1889) to consist of various flies (species of *Helophilus*, *Hotiphila* and *Onesia*), beetles (species of *Donacia* and *Meligethes*) and sweat bees (*Halictus*), the latter being most efficient. Schuster (1907–08) considers the flowers of the European representatives of subsp. *pumilum* to be often self-pollinated, a situation substantiated by Hegi (1912). In any case, the spatial isolation of aquatic habitats decidedly limits the transmission of pollen from one locality to another and permits the development of genetic variants in local areas.

DISPERSAL.—River currents, flood waters and perhaps even fish (Ridley, 1930) effect the dispersal of seeds and uprooted portions of rhizomes in streams and adjacent aquatic areas but the existence of *Nuphar* in isolated ponds and lakes must be the result of some other mechanism. The seeds are neither wind borne nor buoyant in water. However, individual carpels become detached from the decaying fruit and may float for two or three days. Ridley noted that ducks eat these decaying carpels and cited instances where viable seeds have been passed

by these animals. Schuster (1907–08) found the seeds to be digested after passing through the digestive systems of birds and considered the feathers and feet of waterfowl as the means of transport. In either case, the transport of seeds for short distances would be possible.

CHROMOSOMES.—Langlet and Søderberg (1929) report a haploid chromosome number of 17 for *Nuphar advena* (subsp. *macrophyllum*), *N. japonicum*, *N. luteum*, *N. microphyllum* (North American representative of subsp. *pumilum*) and *N. pumilum*, and state that a pair of chromosomes with satellites is characteristic of *N. japonicum*. Heslop-Harrison (1953) reported a diploid chromosome number of 34 in a population of *N. intermedia* (intermediate between subsp. *luteum* and subsp. *pumilum*) in Britain.

MAJOR VARIATIONS.—The European members of *Nuphar* have been segregated into numerous taxa on the basis of such characteristics as the proximity of the leaf lobes, size of flowers, depth and shape of the stigmatic disk, number of stigmatic rays, length of the anthers, color of petals, degree of pubescence, etc. They were recognized by Schuster (1907–08) as comprising two species, "pumilum" of higher latitudes and higher altitudes, and "luteum" of lower latitudes and altitudes, with the presence of "pumilum" in Switzerland and adjacent areas of France and Germany presumed to be the result of glacial influence. Morphologically intermediate forms are discussed by Hegi (1912) as follows: "Zwischen *N.* [*Nuphar*] *luteum* und *N. pumilum* sind verschiedene genau untersuchte Kreuzungs-produkte vorhanden, welche früher als besondere Arten beschriben wurden. Während der Bastard in einzelnen Gegenden neben den Stammeltern vorkommt, erscheint er an andern Stellen ohne dieselben gleichsam als selbstständige Art. Phylogenetische Mittelformen zwischen den beiden Arten gibt es nicht, weshalb es nicht angeht, die beiden Nuphar-Arten nur als Endglieder von Formenreihen einer einzigen Spezies zu betrachten." Even though these intermediate forms do not represent "phylogenetische Mittelformen," they do represent a reticulation of morphological characteristics of such a degree that it seems advisable to consider the involved taxa on an infraspecific basis.

In eastern North America and eastern Asia there occur five-sepaled Yellow Water-Lilies that are very similar to the European representatives of subsp. *pumilum*. These forms have been considered variously as identical with the European plants and as distinct species. The anthers of the European representatives are often slightly shorter, being in extreme cases only one millimeter long, whereas the anthers are often as long as two millimeters in the North American and eastern Asiatic representatives. The stigmatic disk is deeply dentate in all instances, and in the North American representatives, usually deeply tinged with red. The lower surface of the floating leaves is often more or less pubescent, a characteristic which is especially marked in specimens from Switzerland and adjacent areas. The plants are similar in habitat, size and shape of leaves, flowers, sepals, fruit, seeds and rhizomes. Considering the great variation in anther length, presence or absence of red pigments, and the degree of pubescence encountered between other individuals of this genus, these minor differences are not considered sufficient to warrant the recognition of the North American and European repre-

sentatives of subsp. *pumilum* as distinct taxa. This distribution of subsp. *pumilum*, with representatives in eastern North America and in Eurasia, is contrary to the more common distributional patterns. A comparable distribution, on a generic level, may be found in *Corema* D. Don, in which one species is found in North America from Newfoundland to New Jersey, and the other in the Azores, Spain and Portugal, with an extinct species known to have existed in Great Britain (Good, 1953). The distribution of subsp. *pumilum* is more nearly duplicated by *Lobelia dortmanna* L. in which the North American representatives, as treated by McVaugh (1936), are indistinguishable from those with a European distribution as given by Hegi (1918) and Hultén (1950).

In North America a situation similar to that of the subsp. *pumilum*-subsp. *luteum* complex is encountered. The *Nuphar rubrodiscum* segregate, as admitted by various authors, is intermediate between the American representatives of subsp. *pumilum* and the winged-petioled subsp. *variegatum* of Canada and northern portions of United States. Morong (1886) reported that in the Adirondacks these plants produce "no fruit, or scarcely any," and considered it therefore, in this locality, a hybrid between subsp. *pumilum* and subsp. *variegatum*. In Lake Champlain, at Ferrisburg, however, "it bears an abundance of well developed fruit." The "grains of pollen . . . proved, when examined microscopically, as sound as those of either *N. advena* [subsp. *variegatum*] or *N. kalmiana* [subsp. *pumilum*]." Morong thus considers this fertile intermediate as "developed into a good species." Miller and Standley (1912) state that "the characteristics of *Nymphaea rubrodisca* [*Nuphar rubrodiscum*] are quite as constant as in other American species, and no specimens are yet known which show any tendency toward either of the supposed parents." Thus they accept *Nuphar rubrodiscum* as a distinct taxon, but do not accept its hybrid origin as suggested by Morong.

Miller and Standley are quite correct in stating that the characteristics of "rubrodiscum" are as constant as those of other species, for an inconsistency of characteristics seems to be characteristic of the genus! In view of the intermediate nature of any combination of characteristics observed between subsp. *variegatum* and subsp. *pumilum*, and especially in consideration of the complete fertility of these plants in some localities, it seems possible to recognize "rubrodiscum" only as a reticulating segment of a complex polymorphic species.

The winged-petioled subsp. *variegatum*, as well as intergrading with subsp. *pumilum*, intergrades also with the subsp. *macrophyllum* of more or less alkaline and neutral streams and ponds throughout eastern portions of the United States. This has been noted by many authors and is well summarized by Clausen (1949) as follows: "The morphological intergradation of the two populations where their ranges overlap is in accord with the idea that they are only subspecies of a single polymorphic species. This disagreement among taxonomists, some calling them species and others varieties, emphasizes the difficulty in classifying these plants in either of the traditional ways."

The subsp. *macrophyllum* segregate is highly variable, and morphological extremes capable of existing in specialized habitats have evolved. In the Carolinas it passes into the long-leaved subsp. *sagittifolium* of Atlantic coastal rivers. In

South Carolina, eastern and southern Georgia and adjacent Florida, where the leaves are more or less pubescent on the lower surface and assume the floating habit, it passes (through Harper's *Nymphaea fluviatilis*) into the densely pubescent subsp. *orbiculatum* of acidic Coastal Plain ponds in Georgia and adjacent Florida. In western Florida, and coastal areas of Alabama and Mississippi, it passes (through Miller and Standley's *Nymphaea chartacea*) into the subsp. *ulvaceum* of the Blackwater River. The plants in Louisiana and Texas are quite variable, although with counterparts in other areas within the range of subsp. *macrophyllum*, and are perhaps best considered for the present as minor variations of that subspecies.

The *Nuphar* of the Ozark region, subsp. *ozarkanum*, combines characteristics of subsp. *variegatum* (red-tinged sepals and fruit) and subsp. *macrophyllum* (terete petioles and large seeds). Although Miller and Standley (1912) consider the small number of seeds per fruit to be the most striking characteristic of the plant, such few-seeded fruits are often observed in other areas. Furthermore, some specimens exhibit considerable variation in coloration, leaf shape and seed number, approaching subsp. *macrophyllum*. In view of its specialized habitat, however, subsp. *ozarkanum* may be recognized as a segregate very closely related to subsp. *macrophyllum* and subsp. *variegatum*.

The number of sepals is quite variable within this genus. The subsp. *luteum* and subsp. *pumilum* segregates commonly possess five per flower. A colony of subsp. *pumilum* in the Vermilion River, Minnesota, however, has recently been described as possessing from 7 to 14, commonly 13, sepals per flower. Other than subsp. *pumilum*, the American segregates discussed so far commonly possess six sepals per flower. Some specimens of subsp. *variegatum* were observed to have twelve sepals. Specimens of subsp. *ulvaceum* were observed to have anywhere from six to nine sepals per flower and colonies of subsp. *macrophyllum* with seven-sepaled flowers are not uncommon. The subsp. *polysepalum* of Rocky Mountain and Pacific coastal areas of North America usually has seven to twelve sepals, commonly nine; a situation with counterparts in other areas! Its stamens and petals are often deeply tinged with red but not in all instances. The leaf, usually floating and oval with broadly rounded lobes, is quite variable. In some Pacific coastal areas it becomes, like that of subsp. *macrophyllum*, erect with divergent, acute lobes. In northwestern Montana, where it comes in contact with the range of subsp. *variegatum*, leaf and flower characteristics seem to be freely exchanged with that subspecies. The seeds are rather small, narrowly ovoid and are similar to those of subsp. *variegatum*, especially in northwestern Montana. It seems advisable to consider these western plants as no more than a segregate closely related to subsp. *macrophyllum* and subsp. *variegatum*.

FERTILITY:—Little is known concerning intra- and inter-population fertility within the genus *Nuphar*. Populations of subsp. *luteum* and subsp. *pumilum* in Britain were found by Heslop-Harrison (1953) to have a pollen fertility of 97 per cent and 95 per cent respectively. Plants intermediate between subsp. *luteum* and subsp. *pumilum* are reported by Schuster (1907–08) to have 25–85 per cent sterile pollen. Caspary (1869, 1870) reciprocally crossed subsp. *luteum* and subsp.

pumilum. The features of the artificial hybrids were remarkably similar to those of the naturally occurring intermediate forms. Heslop-Harrison (1953) collected 102 seeds from plants intermediate between subsp. *luteum* and subsp. *pumilum*. Seven of these seeds germinated within two months and the "... initial growth was vigorous."

Morong (1886) reported that hybrids between North American and European representatives of subsp. *pumilum* show a physiological difference, but presented no further information.

Plants intermediate between North American representatives of subsp. *pumilum* and subsp. *variegatum*, the *Nuphar rubrodiscum* of Morong, are reported to be almost sterile to completely fertile. Fernald (1942) described a population, × *Nuphar interfluitans*, which is intermediate between subsp. *macrophyllum* and subsp. *sagittifolium*, as "very rarely fruiting, most of the ovaries shriveling."

These examples indicate that barriers to interbreeding do exist within the genus. Whether such barriers are nearly complete and thus evidence of specific rank is questionable, for intermediate forms are abundant in areas where ranges overlap. These intermediates occur with both supposed parents present or, if existing by themselves, are presumably the result of either vegetative reproduction or of numerous hybrid generations.

MINOR VARIATIONS.—Many instances of minor variations in populations of the same taxon were observed in both living and herbarium specimens. Observation of the plants in the field has disclosed variations in the degree of pubescence, shape and habit of the leaves, size of flowers, fruit and seeds, number of stigmatic rays, margin of the stigmatic disk, and color pattern of the flowers and fruit. Entire colonies and sometimes most of the plants in an aquatic area were found to exhibit a singular pattern of variation. For example, in the New River, where it is crossed by Georgia Highway 37, three adjacent colonies differed in the position of the leaf lobes. In one, the lobes were widely spread, in another, more or less overlapping, and in the third, intermediate in position. Even more striking in this regard were the plants observed in a ditch along U. S. Highway 17 east of Jacksonboro, South Carolina. Most of the plants exhibited a brown-red band around the middle of the fruit, a rather unique color pattern also noted by R. L. Wilbur and G. L. Webster [specimen no. 2847 (MICH)] in an adjacent locality.

Such singular patterns of variation in isolated areas are of local importance and, when studied thoroughly, should be of great value in elucidating phylogenetic relationships among the numerous variants of this genus. It would be futile and most confusing, however, if all variants and intermediates were to be formally recognized by systematic taxonomy. Therefore, only these variants that coincide with geographical or ecological features are recognized as subspecies. In this manner, the identity of the extremes is maintained, yet plants of an intermediate nature are neither unexpected nor confusing.

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A NEW HYBRID OAK FROM THE PIEDMONT OF NORTH CAROLINA

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Three seasons of observation and study of an oak found in the swamp of Buffalo Creek near Greensboro in Guilford County, N. C., has led to the conclusion that it is a hybrid of *Quercus lyrata* Walt. by *Q. michauxii* Nutt. At first, I was

under the impression that I had found *Quercus bicolor* Willd. but from a study of collected specimens (*Melvin 2001* and subsequent collections of September 24 and 26, 1954; and October 9 and 26, 1954) Dr. H. R. Totten pointed out the lack of soft, downy, pubescence beneath the leaves and the absence of the long fruiting peduncle characteristic of that species. He further suggested that I had found a hybrid. *Quercus michauxii* was unquestionably one of the parents since no other species with chestnut-like leaves occurred in the vicinity. *Quercus alba* and *Q. stellata* were lacking in the immediate area, but *Q. lyrata* of the form *viridis* Trel. was abundant. The fruit offers further proof that only *Q. lyrata* could have been the other parent, for the acorn cup bears the blunt and rugged lower scales that are found only in that species of the white oak group native to our piedmont. In addition, the cup encloses from one-half to two-thirds of the acorn, approaching the sometimes fully enclosed acorn of *Q. lyrata.*

A natural seedling of the hybrid which I transplanted to my grounds in Pleasant Garden produces leaves that occasionally show a sinus separating the shorter basal lobes from the larger apical lobes, approaching the leaf form of *Q. lyrata.* This characteristic was found to exist in the parent, but less pronounced. Collection *2002*, July 2, 1955, shows this separation of lobes by the sinus in the leaves of the seedling. Seeds of the hybrid were planted in the spring of 1955. Six plants were obtained and four of these survived. Two of these resemble very closely *Q. michauxii* while the other two are almost indistinguishable from seedlings of *Q. lyrata.*

Quercus × totteni hybr. nov.

Hybrida naturalis inter Quercum lyratam et Quercum michauxii. Cortice trunci parum squamato, non argenteo ut in Quercu michauxii; ramulis flexuosis ut in Quercus lyrata; foliis inversum ovatis, in basi acutis, singulis detatis, altius sectis et dispositis minus ordinate quam in Quercu michauxii, lobis inferioribus nonnumquam separatis sinu e superioribus ut in Quercu lyrata, superficie infra viridi ut in forma viridis Quercus lyratae vicine praevalentis; fructu sessili aut cum brevibus pediculis ut in parentibus ambobus; calyce tam alto quam glande querno parte dimidia aut partis trientibus duobus, inferis scamis horridis ut in Quercu lyrata, glandibus quernis ovatis ut in Quercu michauxii.[1]

A natural hybrid between *Quercus lyrata* and *Quercus michauxii.* Trunk with slightly flaky, light gray bark, not silvery as in *Q. michauxii*; twigs flexuous as in *Q. lyrata*; leaves obovate, acute at the base, severally dentate, more deeply cut and less regularly arranged than in *Q. michauxii*, the basal lobes sometimes separated from the upper by a sinus as in *Q. lyrata*, surface beneath green as in the form *viridis* of *Q. lyrata* prevalent in the area; fruit sessile or short-peduncled as in both parents; cup one-half to two-thirds as high as acorn, low scales rugged as in *Q. lyrata*; acorns ovoid as in *Q. michauxii.*

TYPE LOCALITY: Swamp of Buffalo Creek, Guilford County, N. C., 1954.

TYPE SPECIMEN: *Melvin 2001* (type: NCU)

So far as I have been able to learn, no hybrid of *Quercus michauxii* by *Q. lyrata* has been recorded and it pleases me to name it *Quercus × totteni* in honor of Henry Roland Totten who first recognized the tree as a hybrid. Dr. Totten has spent a lifetime in the study of the trees of the southeastern states and I know of no one more deserving of this small honor.

[1] I wish to thank Prof. J. Arthur Dunn for this Latin description.

A NEW SPECIES OF *WORONINA*, AND *SORODISCUS COKERI* EMENDED [1]

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The Plasmodiophoraceae are known chiefly as parasites of flowering plants. The only known members of the group which parasitize fungi are the following: *Octomyxa achlyae* (Couch, Leitner and Whiffen, 1939) and *O. brevilegniae* (Pendergrass, 1948) on Saprolegniaceae; *Sorodiscus cokeri* (Goldie-Smith, 1951) on species of *Pythium*; and *Woronina polycystis* (Cornu, 1872) on Saprolegniaceae, only recently shown to have a place in the Plasmodiophoraceae (Goldie-Smith, 1954). The species described below, on *Pythium*, is a fifth member of this family occurring as a parasite of fungi.

Woronina pythii sp. nov.

Fungus parasiticus in hyphis Pythii; tumoribus semper disjunctis per septa, plerumque catenatim. Nucleis primorum plasmodiorum passis cruciformes divisiones. Maturo plasmodio formante sorum zoosporangiorum vel sporarum perdurantium. Zoosporangiis globosis vel ovoideis, 4.9–8.8μ in diam.; zoosporis biflagellatis, posteriore flagello longo, anteriore brevi. Sporis perdurantibus 3.7–5.6μ in diam., levibus, cum parietibus incrassatis; cystosoro globoso, aureo-brunneo.

Obligate parasite in species of *Pythium*, causing galls which are always delimited by septa, often in catenulate series. Nuclei undergoing cruciform divisions during vegetative stages of plasmodium. Mature plasmodium forming a sorus of zoosporangia, or a cystosorus composed of resting spores. Zoosporangia thin-walled, spherical or ovoid, about 4.9–8.8μ in diam. Zoospores biflagellate, with one long posterior and one short anterior flagellum; discharged through papillae formed only on some sporangia on the periphery of the sorus; encysting on the hyphae and other organs of the host, and germinating with a short, swollen penetration tube. Resting spores about 3.7–5.6μ in diam., smooth, thick-walled, loosely associated in a cystosorus, forming a sphere or flattened spheroid with its greatest diameter usually less than the diameter of the gall containing it, golden-brown in color. Sporangial and resting spore membranes without cellulose, as shown by a negative reaction with chlor-iodide of zinc.

Isolated from a soil sample collected by Dr. W. C. Coker from damp swale, near oaks and bamboo, at Fort Lauderdale, Fla., Feb. 18, 1949.

The Host.—The original host of *W. pythii* appears to be a strain of *Pythium proliferum*, but a different one from the original host of *Sorodiscus cokeri*. Sporangia are abundant in both and cover a similar range in size, though averaging slightly larger in the *Woronina* host than in the *Sorodiscus* one: in the former, they are mostly 29–38μ in diameter, ranging from 21.0μ to 46.2μ; in the latter they are mostly 29–33μ in diameter, with a range of 22.5μ to 42.2μ. Newly-encysted zoospores of the former measure 9.8–11.0μ; those of the latter, 8.9–10.6μ,

[1] Some of this work was done in partial fulfillment of the requirements for the Ph.D. degree in the Department of Botany, University of North Carolina.

but most have been found to range from 9.6μ to 10.3μ. Numerous oogonia are formed by the *Woronina* host on most media, about 15–24μ in diameter, mostly 19.0–22.8μ; the oospores are about 12.4–19.0μ, mostly about 17.1μ in diameter. Oogonia of the *Sorodiscus* host have been found only once; the oospore measured 18.7–26.2μ, mostly about 22μ.

OTHER STRAINS OF THE PARASITE: (1) FROM TEXAS.—Collected by R. M. Johns in a soil sample from the site of the Old Southerland Springs Hotel, Old Southerland Springs, Wilson Co., Texas, Aug. 4, 1951. In this strain, the cystosori are more noticeably flattened and their golden-brown color is even more conspicuous. They are fewer and average larger than in the Florida strain. In the Texas strain, the largest cystosorus measured was 82μ in diameter, and the largest cystosoral gall was 102μ in diameter. Corresponding figures for the Florida strain are 46.2μ and 67μ, respectively. This difference is to be correlated with the fact that the host of the Texas strain forms fewer, larger, sporangia. For *W. pythii*, the two hosts are interchangeable.

(2) FROM LOUISIANA.—Collected by the author from a roadside ditch near Baton Rouge, on Rte. 30, Apr. 15, 1954. This strain has not been studied in detail.

METHODS OF CULTURE.—The same methods as for *S. cokeri* were used with *W. pythii*, which responded in a very similar way. Stock cultures were maintained in petri dishes by adding fresh seeds, at intervals, to growths of the infected host on hemp seeds. Cultures as clean as possible were obtained, as in *S. cokeri*, by using well-washed infected material as inoculum for *Pythium* cultures previously cleaned by growth through three per cent plain agar. Sometimes a single zoosporangial sorus, which had been rolled about with sharp needles on plain agar to free it from other organisms, was used as inoculum. As described previously (1956, p. 161), storage at 18°C. of hemp seed cultures in test-tubes about one-third full of water is a convenient and usually reliable method for both parasites. The use of sterile soil instead of water offered no advantage; if either dried out, the parasite was usually "lost" although the host might be recoverable. This is probably because the resting spores of the Plasmodiophoraceae require special conditions for germination that are not well understood. In moist cultures, renewed growth often takes place from zoosporangia, which seem to be capable of remaining dormant for long periods if they are not allowed to dry.

CHARACTERISTICS.—The development of *W. pythii* closely resembles that of *W. polycystis* and the two species of *Octomyxa*, and is so similar to that of *S. cokeri*, in the early stages of the first-formed galls, that the two organisms are almost indistinguishable, especially when observed on identical hosts. The mycelium was stained *in toto* with crystal violet, according to the schedule used for *S. cokeri* (1951, p. 117) and the cruciform nuclear figures characteristic of the vegetative stages of the Plasmodiophoraceae were observed. In figure 1, a gall contains in the center a small plasmodium with one large nucleus, and several disorganizing nuclei of the host are also evident. The large size of the nuclei of the parasite, in comparison with those of the fungi in which they develop, is a notable feature of both species of *Woronina* as well as of *S. cokeri*. In figure 2, the single nucleus of a plasmodium is undergoing protomitosis and has reached the "ring-

of-saturn" stage. Figure 18 shows a plasmodium with nuclei at the cruciform stage. "Akaryote" stages (Fig. 19) and the mitoses preceding zoospore formation have also been seen. Stained material quite often reveals the presence of one or more small uninucleate plasmodia towards the side of a gall in which most of the central space is occupied by a large multinucleate one. Whereas it is more common in *W. pythii* than in *S. cokeri* to find several plasmodia in a single gall (Fig. 16, 17, 20, 21) it seems that unless the two or more plasmodia are far enough apart to split between them the host's protoplasm present in the gall (Fig. 20), one plasmodium gets ahead in development; or, possibly, the contents of spores entering later are unable to develop in competition with a plasmodium that is already established.

Woronina pythii may be distinguished from *S. cokeri* in quite early stages, however, by its appearance in chains of galls formed in basipetal succession. Also, hypertrophy of the host is conspicuous, many of the galls attaining a size never observed in the sporangia of the uninfected host. The galls are mostly 25–45μ in diameter but may be as large as 67μ; the sporangia of a healthy culture are mostly 29–38μ, the largest found being 46.2μ in diameter. *Sorodiscus cokeri* was originally described as "causing little or no hypertrophy," but, as shown later in this paper, hypertrophy may indeed be caused, a fact established by the study of two strains in addition to the original one. The description has accordingly been emended.

The cystosori, developing in older cultures, serve at once to separate *W. pythii* from *S. cokeri*. The golden-brown balls of thick-walled spores (Fig. 6, 33–35) are strikingly distinct from the groups of 2, 3, 4, or more, single-layered discs of *S. cokeri* (Fig. 14, 15). Unlike that of *S. cokeri*, the cystosorus of *W. pythii* does not extend across the full diameter of the gall containing it. Moreover, if the cystosori are mounted on a slide and pressed gently under a coverslip, the spores are easily separated (Fig. 7). When *S. cokeri* is treated in this way, the arrangement of the spores in the discs remains unchanged and the discs themselves are not easily separable. Furthermore, the spores of *W. pythii* do not fall apart into groups of four as in *Tetramyxa*, or of eight as in *Octomyxa* (Couch, Leitner and Whiffen, 1939, fig. 4, 5), but separate out individually as in *W. polycystis*. In *W. polycystis* the spore-balls are more nearly spherical than in *W. pythii*, but the cystosorus may also be represented by elongated, irregular aggregations of spores in cylindrical segments of the host which are scarcely hypertrophied. These elongated cystosori are not found in *W. pythii*. The hyphae of species of *Pythium* are much narrower than those of most of the Saprolegniaceae, the hosts of *W. polycystis*, and it seems that the parasite cannot complete its development in them without some lateral expansion into a swelling, although this may be quite small.

The genera of the Plasmodiophoraceae are distinguished according to the arrangement of the spores in the cystosorus. Although *W. pythii* resembles *S. cokeri* in the early stages of its life cycle, and similarly occurs on species of *Pythium*—even identical strains—it is more closely allied to *W. polycystis*, and most differences from this species are probably related to differences in their hosts, such as the greater width of the hyphae and the larger size of the reproductive

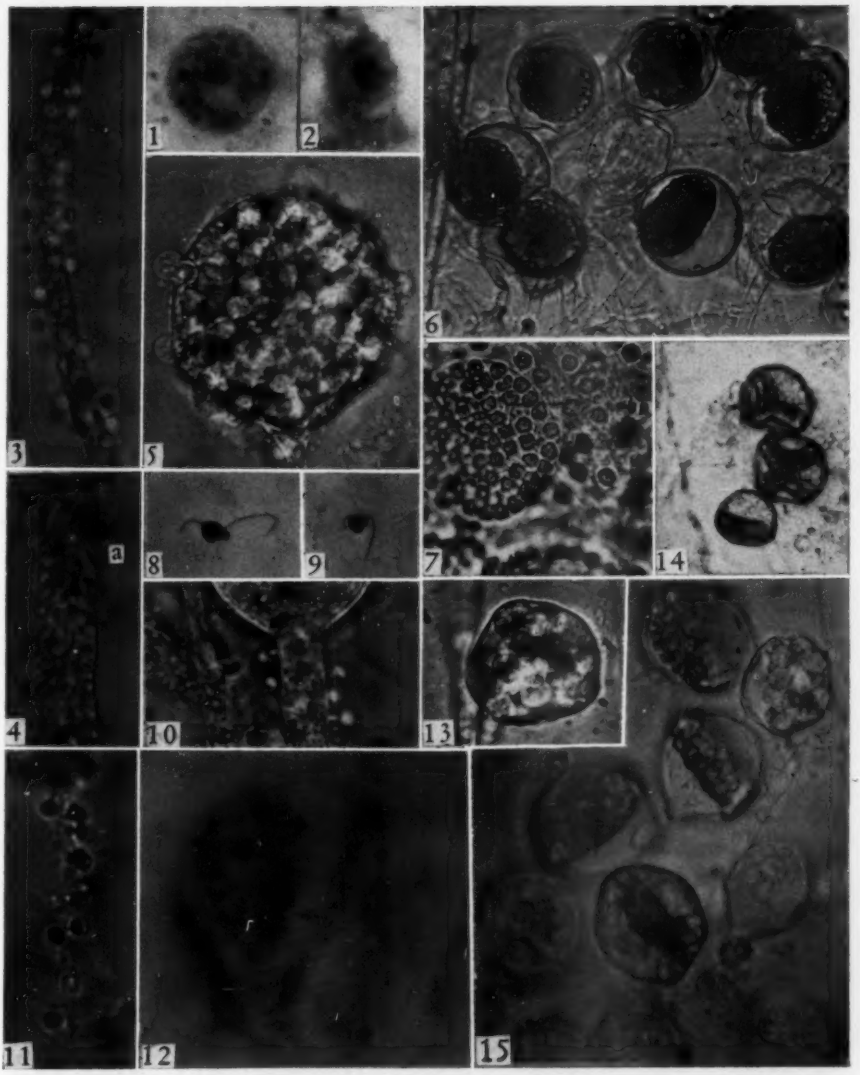

FIG. 1–8. *Woronina pythii* on *Pythium proliferum*. FIG. 1–4, 8, Florida strain; FIG. 5–7, Texas strain. FIG. 1. Gall containing a uninucleate plasmodium. ×1000. Material fixed in Randolph's modified Navashin fluid and stained with gentian violet. FIG. 2. Uninucleate plasmodium, the nucleus at the "ring-of-saturn" stage of division. ×4400. Fixed and stained as above. FIG. 3. Zoospores newly encysted on a hypha. ×900. FIG. 4. Zoospores encysted and germinating on a hypha; *a*, encysted spore with contents passing through bulbous germ-tube. ×1000. FIG. 5. Zoosporangial sorus with discharge papillae. ×750. FIG. 6. Cystosori in face and side views, showing flattened shape. ×400. FIG. 7. Cystosorus lightly compressed under a coverslip, separating into individual spores. ×670. FIG. 8. Zoospore fixed with osmic acid fumes and stained with gentian violet. ×1300.

FIG. 9–15. *Sorodiscus cokeri* on *Pythium proliferum* (FIG. 9, 12, 13, 15) and *P. graminicolum* (FIG. 10, 11, 14). FIG. 9. Zoospore fixed and stained as in Fig. 8. ×900. FIG. 10, 11. Encysted germinating spores on organs of host. ×1000. FIG. 12. Plasmodium with nuclei at cruciform stage of division, stained with gentian violet. ×1000. FIG. 13. Zoosporangial sorus. ×700. FIG. 14. Cystosori with 2, 3, and 4 discs. ×400. FIG. 15. Zoosporangial and cystosoral galls. ×620.

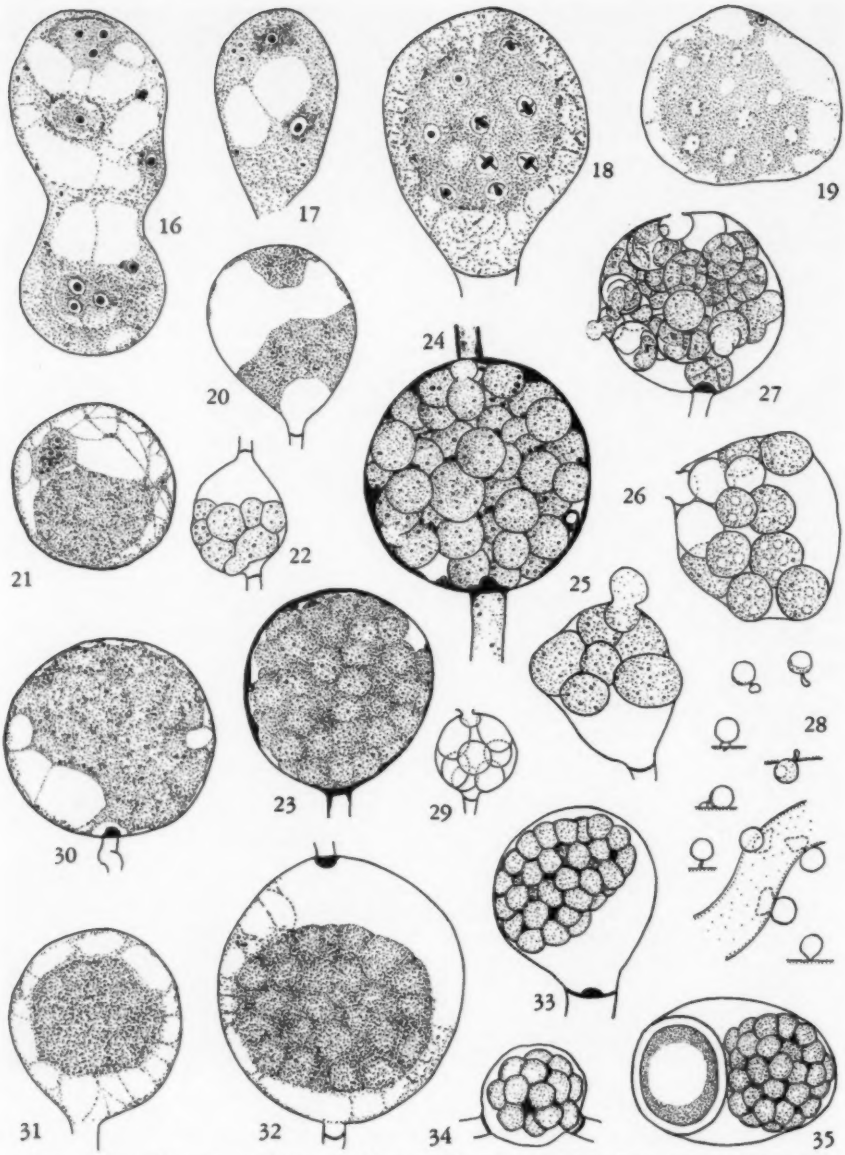

FIG. 16–35. *Woronina pythii* on *Pythium proliferum* (the original host; except FIG. 26, a strain of *P. proliferum* from South Carolina). FIG. 16–20. Material fixed in Randolph's modified Navashin fluid and stained with gentian violet. FIG. 16. Several plasmodia in a gall. ×580. FIG. 17. Two uninucleate plasmodia in a gall. ×580. FIG. 18. Plasmodium with nuclei at cruciform stage of division. ×700. FIG. 19. Beginning of "akaryote" stage. ×580. FIG. 20, 21. Galls each containing two plasmodia. ×440. FIG. 22. Zoosporangial sorus, one sporangium forming an exit tube. ×440. FIG. 23. Young zoosporangial sorus. ×525. FIG. 24. Mature zoosporangial sorus with much refractive material against the inside of the host wall. ×525. FIG. 25. Zoosporangial sorus, one sporangium with large exit "bubble." ×700. FIG. 26. Vacuolate stage of sporangia. ×700. FIG. 27. Sorus discharging zoospores. ×525. FIG. 28. Encysted zoospores; some germinating, their contents inside the host wall. Diagrammatic. FIG. 29. Empty zoosporangial sorus. ×440. FIG. 30–32. Early stages in development of cystosori. ×525. FIG. 33, 34. Mature cystosori. ×580. FIG. 35. Cystosorus in oogonium with mature *Pythium* oospore. ×525.

organs of the Saprolegniaceae, than those of *Pythium*. *Woronina polycystis* averages larger than *W. pythii*, at all stages of its life cycle; and its galls more often contain many plasmodia. The formation of chains of galls by the segmentation of the hyphae of the host occurs in both species, an important feature distinguishing them from *Octomyxa* and *Sorodiscus*. Segmentation is a natural occurrence in many of the Saprolegniaceae, in the formation of gemmae; it is much less common in healthy *Pythium* hyphae, in which septa are formed only upon the delimitation of reproductive organs and, in older parts, separating off the empty basal regions from actively growing parts of the hyphae.

In *W. polycystis*, an encysted zoospore forms a relatively long, curved tube on germination. In *W. pythii*, the germ-tube is short and enlarged into a bulbous swelling, like a subspherical "stalk" between the spore-cyst and the attacked hypha (Fig. 4a, 28). After the passage of the contents into the hypha, the tube collapses a little and appears even more stalk-like, or may collapse altogether so that the empty cyst seems to rest directly on the hypha again. This type of germination, at first overlooked, has been found in *S. cokeri* also (Fig. 10, 11). Encystment and the formation of a "stalk" were described and illustrated by Fischer (1882) for *W. polycystis*, and the transference of this organism to the Plasmodiophoraceae (Goldie-Smith, 1954) made it the first member of the family in which this type of behavior had been recorded. Its observance in two additional members, *S. cokeri* and *W. pythii*, is of considerable importance, since it is frequently stated that in the Plasmodiophoraceae the zoospore penetrates naked, without encystment.

As observed in *W. polycystis* by Fischer, the emptying of the spores is not controlled by the availability of nourishment; they will empty their contents into a hypha containing practically no protoplasm, although no further development can take place. Galls are frequently seen with a variable number, sometimes very many, irregularly-shaped lumps of highly refractive material immediately within the wall (Fig. 23, 25) which are still present after the emptying of the sporangia. With chlor-iodide of zinc, these show the same bluish-purple color as that of the deposition that is frequently present on the septum, and supposedly contain cellulose, or are covered by it. Their exact nature is undetermined, but it has been observed that an encysted zoospore of the parasite often lies immediately above one of them, outside the wall. It seems most likely that they are the remains of superfluous plasmodia unable to develop further. This is probably an unnatural condition due to the liberation of enormous numbers of zoospores in a short time within the confines of a petri dish and without the competition of other organisms.

The zoospores of *W. pythii* have been stained with crystal violet after fixation with osmic acid fumes (Fig. 8). This treatment shows that, as in *S. cokeri* (Fig. 9), the long, posterior flagellum bears a whiplash, whereas the short, anterior one ends bluntly or in a slight point. In *W. polycystis* each flagellum clearly ends in a whiplash.

HOST RELATIONSHIPS.—The ability of *W. pythii* to infect other species and strains of *Pythium* was investigated, as in *S. cokeri*, by the following method: Single zoosporangial sori are dissected from a vigorous, well-washed culture and

transferred in a capillary pipette to a dish of three per cent plain agar; the sorus is freed from other organisms, particularly the zoospores of the host, by rolling it around on the agar, and is then transferred on a small block of agar to a dish containing a pure culture of *Pythium*. In this way, the following were successfully inoculated: *P. aphanidermatum; P. catenulatum; P. debaryanum; P. irregulare; P. monospermum; P. proliferum* (several strains, including the original host of *S. cokeri*); *P. pulchrum; P. ultimum;* and *P. undulatum*. Some species are much more susceptible than others, and are easily infected. Infection of *P. monospermum* and *P. undulatum* was obtained only after many attempts. So far, *P. dissotocum* and *P. graminicolum* have resisted infection. The wide host range of *W. pythii* and *S. cokeri* and their ability to grow on the *same* host are of great interest, since the occurrence of a parasite on a new host is sometimes regarded as evidence of its nature as a new variety or even a new species.

Members of other groups can be tested more easily, since their hyphae are readily distinguished among those of *Pythium*; it is therefore not necessary to dissect out single sori; instead, an entire culture containing the parasite can be placed in each dish with the organism to be tested, which is then examined at intervals for infection. The following all proved resistant: Leptomitaceae—*Apodachlya brachynema*. Saprolegniaceae—*Achlya americana; A. apiculata; A. dubia; A. klebsiana; A. racemosa; Saprolegnia diclina; S. litoralis; S. monoica; Isoachlya unispora; Thraustotheca clavata; T. primoachlya; Aphanomyces laevis; Brevilegnia linearis; Dictyuchus* sp. Blastocladiaceae—*Allomyces javanicus* var. *macrospora*.

Sorodiscus cokeri Goldie-Smith emend.

Fungus parasiticus in hyphis Pythii. Maturo plasmodio formante sorum zoosporangiorum vel sporarum perdurantium. Zoosporangiis globosis vel ovoideis, 5.3–8.8μ in diam. Zoosporis biflagellatis, posteriore flagello longo, anteriore brevi, 4–11, pleurumque 8 vel 9, in zoosporangio. Sporis perdurantibus 3.1–4.1μ in diam., levibus, cum parietibus incrassatis; sporis ordinatis in discibus, crassitudinis singularium sporarum, 2–4 vel ampliis in cystosoro, firmiter compactis.

Obligate parasite on species of *Pythium*. Naked plasmodium undergoing cruciform nuclear divisions during vegetative growth; at maturity partly or occasionally wholly filling the swelling, and dividing into zoosporangia or resting spores. Zoosporangia thin-walled, spherical to ovoid, about 5.3–8.8μ in diam. Zoospores biflagellate, with one long posterior and one short anterior flagellum; 4–11, usually 8 or 9, in a sporangium; discharged through papillae formed only on some sporangia on the periphery of the sorus; encysting on the hyphae and other organs of the host, germinating with a short, swollen penetration tube external to the host wall. Resting spores about 3.1–4.1μ in diam., smooth, thick-walled, closely pressed together in circular or ovoid discs one spore thick. Discs frequently paired, forming curved, two-layered plates; or in threes or fours, giving an appearance in section of Y- or H-shaped figures, respectively; or in larger groups. Sporangial and resting spore membranes without cellulose, as shown by a negative reaction with chlor-iodide of zinc.

The above description differs from the original (Goldie-Smith, 1951) in that the occurrence of hypertrophy is not excluded, and the formation of a germ tube by the encysted zoospore, and the possibility of the formation of more than four discs in a cystosorus, are recognized.

On the original host, an isolate of *Pythium proliferum* from Florida, the parasite does not induce the formation of swellings larger than the sporangia formed by the uninfected fungus. Hence its description as "causing little or no hypertrophy." However, the parasite may cause the formation of a greater number of swellings than in a healthy sporangial culture, a large proportion of which are in the lower half of the total range in size. Furthermore, these swellings are often irregular in shape and intercalary in position, unlike the spherical, terminal sporangia of the host. Thus it may be argued that a type of hypertrophy is in fact caused, since the host is stimulated to develop swellings foreign to its nature. The study, subsequently, of two other isolates has established that hypertrophy in its usual sense also occurs; that is, the parasite may induce the formation of greater enlargements than are normally produced by the host.

ADDITIONAL ISOLATES: (1) FROM SOUTH CAROLINA.—Isolated from a soil sample collected by Dr. J. N. Couch, north of Calhoun Falls, S. C., on Rte. 72, Apr. 22, 1951. Host: *Pythium graminicolum*. This species of *Pythium* forms sporangia of the inflated filamentous type, up to 36μ in diameter, in toruloid complexes. Galls caused by the presence of the parasite, however, have been found up to 59.2μ in diameter. They are usually terminal on lateral branches which widen quite gradually into sac-like swellings; these consequently have an elongated pyriform shape, and are entirely unlike any organs normally formed by the uninfected fungus. This isolate thus demonstrates very clearly the ability of *S. cokeri* to cause hypertrophy.

(2) FROM TEXAS.—Isolated from a soil sample collected by R. M. Johns from south (mesquite) pasture, L. E. Johns farm, about 12.5 miles w. s. w. of Floresville, Wilson Co., Texas, Dec, 24, 1951. Host: *Pythium catenulatum*. In the individual spherical or pyriform swellings, 10–20μ in diameter, especially the smaller ones, a cystosorus will often consist of two discs pressed together, as commonly found in the Florida isolate. In the irregular aggregations of swellings, however, individual ones of which may be inflated up to 42μ by the presence of the parasite, the configuration of the cystosorus is much more complicated, the number of discs being greater. When transferred to *P. graminicolum* this strain also causes large pyriform swellings; as many as seven discs of resting spores have been counted in one of these galls.

SUMMARY

Woronina pythii is described, with a wide host range on species of *Pythium*, and it is compared with other members of the Plasmodiophoraceae occurring as parasites of fungi. The description of *Sorodiscus cokeri* is emended to include the possibility of hypertrophy, and of the formation of more than four discs in a cystosorus. It is shown that in both organisms the encysted zoospore forms a short,

distally swollen germ-tube on germination; and considerable significance is attached to the fact that both organisms will develop in the same host.

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